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***Orientattractis brycini* sp. nov. (Nematoda: Atractidae)
from characiform freshwater fishes in Gabon, Africa**

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Abstract: The nematode *Orientattractis brycini* sp. nov. (Atractidae) is described from the intestine of *Brycinus macrolepidotus* Valenciennes (Alestidae) and *Xenocharax spilurus* Günther (Distichodontidae) collected in two localities from Gabon, Africa. The new species is characterized by the presence of four submedian lips with well-sclerotized pieces armed with two recurved pointed spines and one median large spine on their distal part, along with two smaller spines posterior to amphidial pores. It differs from its congeners mainly in the length of both spicules, gubernaculum, presence of two lateral spines posterior to amphids, distribution and number of caudal papillae. An emended generic diagnosis is provided. This is the eighth species in the genus *Orientattractis*, the fourth from fish hosts and the first from Africa, which expands its geographical distribution.

Keywords: New species - nematode - *Brycinus* - *Xenocharax*.

INTRODUCTION

The family Atractidae Railliet, 1917 includes 26 genera separable into two groups according to the type of ovaries: *Atractis* Dujardin, 1845, *Buckleyattractis* Khalil & Gibbons, 1988, *Cobboldina* Leiper, 1911, *Crossocephalus* Railliet, 1909, *Cyrtosomum* Geddoelst, 1919, *Diceronema* Gibbons, Knapp & Krecek, 1995, *Grassenema* Petter, 1959, *Labeonema* Puylaert, 1970, *Labiduris* Schneider, 1866, *Leiperenia* Khalil, 1922, *Klossinemella* Costa, 1961, *Monhysterides* Baylis & Daubney, 1922, *Orientattractis* Petter, 1966, *Paraorientattractis* Gibbons, Khalil & Marinkelle, 1997, *Parattractis* Sarmiento, 1959, *Pneumottractis* Bursey, Reavill & Greiner, 2009, *Podocnemattractis* Gibbons, Khalil & Marinkelle, 1995, *Proattractis* Caballero, 1971, *Pseudattractis* Yamaguti, 1961, *Pseudocyrtosomum* Gupta & Johri, 1987, *Rhinoceronema* Mondal & Manna, 2013, *Rhinoclemmysnema* Gibbons & Platt, 2006, and *Rondonia* Travassos, 1920 are in the monodelphic group; whereas *Fitzsimmonsnesia* Petter, 1966, *Nouvelnema* Petter, 1959, *Probstmayria* Ransom, 1907, form the didelphic group (Adamson & Baccam, 1988; Bursey & Flanagan,

2002; Gibbons, 2010; Mondal & Manna, 2013). Of these, *Proattractis* was synonymized with *Klossinemella*, while *Cyrtosomum* and *Pseudattractis* were synonymized with *Atractis* (see Baker, 1987; Moravec & Thatcher, 1997), although Bursey & Flanagan (2002) retained both genera as valid.

During a short visit to the Muséum d'histoire naturelle de Genève in 2012, the examination of parasitic nematodes collected from freshwater fishes in Gabon, Africa, revealed the presence of very peculiar attractid specimens. These parasites were found in two characiform fishes, *Brycinus macrolepidotus* Valenciennes (Alestidae) and *Xenocharax spilurus* Günther (Distichodontidae) and belong to an unknown species of *Orientattractis*, which is described herein.

Brycinus macrolepidotus and *X. spilurus* are freshwater fishes that inhabits rivers and lakes in Lower Guinea, from Cameroon to the Chiloango River Basin, the Nile system and the Democratic Republic of Congo. They feed on insects, crustaceans and vegetation (Froese & Pauly, 2016).

MATERIAL AND METHODS

Fishes were collected by angling in 2 localities from the Franceville area, Southeast Gabon, in November 2010. All nematode specimens recovered were washed in physiological saline, fixed in hot 4% formaldehyde solution and cleared in different ratios of glycerine-water mixture for light microscopy. For scanning electron microscopy (SEM), specimens were postfixed in 1% osmium tetroxide (in phosphate buffer), dehydrated through a graded acetone series, critical-point-dried and sputter-coated with gold; they were examined using a JEOL JSM-7401F scanning electron microscope at an accelerating voltage of 4 kV (GB low mode). Drawings were done with the aid of a camera lucida. All measurements are in micrometers, unless otherwise indicated. Scientific names of fishes follow Froese & Pauly (2016). All collections were made in the frame of a Scientific Research Convention between the Centre International de Recherches Médicales de Franceville (CIRMF) and the Muséum d'histoire naturelle de Genève (MHNG) with the research permit AR0017/09/MESRSDT/CENAREST/CG/CST/CSAR.

TAXONOMIC PART

Family Atractidae Railliet, 1917

Genus *Orientattractis* Petter, 1966

Type species: *O. levanhoai* Petter, 1966

Emended generic diagnosis: Small nematodes with a complex structure of the apical extremity. Oral opening surrounded by 6 (2 lateral and 4 submedian) poorly-developed lips. One or two circlelets of oral papillae. Each submedian lip bearing a chitinous piece formed by two well-sclerotized, recurved, pointed spines and a single large median spine. Lateral lips small, supporting large amphids; two small spines posterior to each amphidial pore present or not. Grooves or narrow lateral alae present, extending from first third of esophagus to posterior end of body, but not reaching tail tip. Esophagus divided in a cylindrical corpus, elongated isthmus, and posterior, well-developed or not, valved bulb. Nerve ring surrounding isthmus at its anterior end. Deirids small, knob-like, somewhat anterior or at level of nerve ring. Excretory pore at mid-length of corpus or slightly anterior to esophageal bulb. Tail long and thread-like. Males with two unequal, similar spicules and small gubernaculum. Females monodelphic, viviparous, with vulva near anus. Parasites of freshwater turtles, frogs and fish.

***Orientattractis brycini* sp. nov.**

Figs 1-3

Deposition of specimens: Holotype (MHNG-INVE-91071), allotype (MHNG-INVE-91072) and pa-

ratypes (MHNG-INVE-91073) in the Muséum d'histoire naturelle, Geneva. – Paratypes in the Helminthological Collection of the Institute of Parasitology, Biology Centre, Czech Academy of Sciences, České Budějovice (Cat. No. N-1072).

Type host: *Brycinus macrolepidotus* Valenciennes (Alestidae, Characiformes) (Body length 21.4 cm).

Other host: *Xenocharax spilurus* Günther (Distichodontidae, Characiformes) (Body length 15.5-20.2 cm).

Site of infection: Intestine.

Type locality: Bridge on Ogooué River, Haut-Ogooué, Gabon (01°38'24"S; 13°31'48"E; elev. 300 m), collected on 28/11/2010.

Other localities: Mpassa River, near Hotel Poubara, Franceville, Haut-Ogooué, Gabon (01°37'12"S; 13°36'00"E; elev. 300 m), 30/11/2010.

Prevalence and intensity: *Brycinus macrolepidotus*: prevalence 25% (1 fish infected/4 examined), mean intensity 24 nematodes (range 24). *Xenocharax spilurus*: 43% (3/7), 4.3 (2-8).

Etymology: The specific name relates to the generic name of the fish host (i.e., *Brycinus*).

Description

General: Whitish, small-sized nematodes, with cuticle finely transversely striated. Anterior end rounded, posterior end with very slender, long, pointed tail (Fig. 1A, E). Oral opening rhomboid or quadrangular, with 2 lateral and 4 submedian poorly-developed lips (Figs 1D, 2A, B). Each submedian lip bearing one large spherical papilla and external pair of well-sclerotized, recurved, pointed spines joined at the base and a single large median spine. Lateral lips supporting large amphids; two small spines posterior to each amphidial pore present (Figs 1D, 2A-D). Lateral grooves extending from first third of esophagus to posterior end of body, but not reaching tail tip (Figs 1E, G, 2F). Esophagus divided in a cylindrical corpus, elongated isthmus, and posterior, well-developed, valved bulb (Fig. 1A, B). Nerve ring surrounding isthmus at its anterior end. Deirids small, knob-like, somewhat anterior or at level of nerve ring (Figs 1A, B, 2E). Excretory pore anterior to esophageal bulb (Fig. 1A, B). Intestine straight. Rectum a hyaline tube.

Male (22 specimens, measurements of holotype in parentheses): Length of body 2.58-3.07 (3.04) mm, maximum width 52-93 (72). Length of corpus 130-163 (150), of isthmus 289-346 (305); entire esophagus 436-507 (455). Width of esophageal bulb 33-47 (43). Nerve ring, excretory pore, and deirids 162-226 (178), 294-350 (310), and 175-199 (189), respectively, from anterior end of body. Eight pairs of caudal papillae: 1 subventral precloacal pair, 3 subventral adcloacal pairs, close to each other (one pair anterior to cloacal opening,

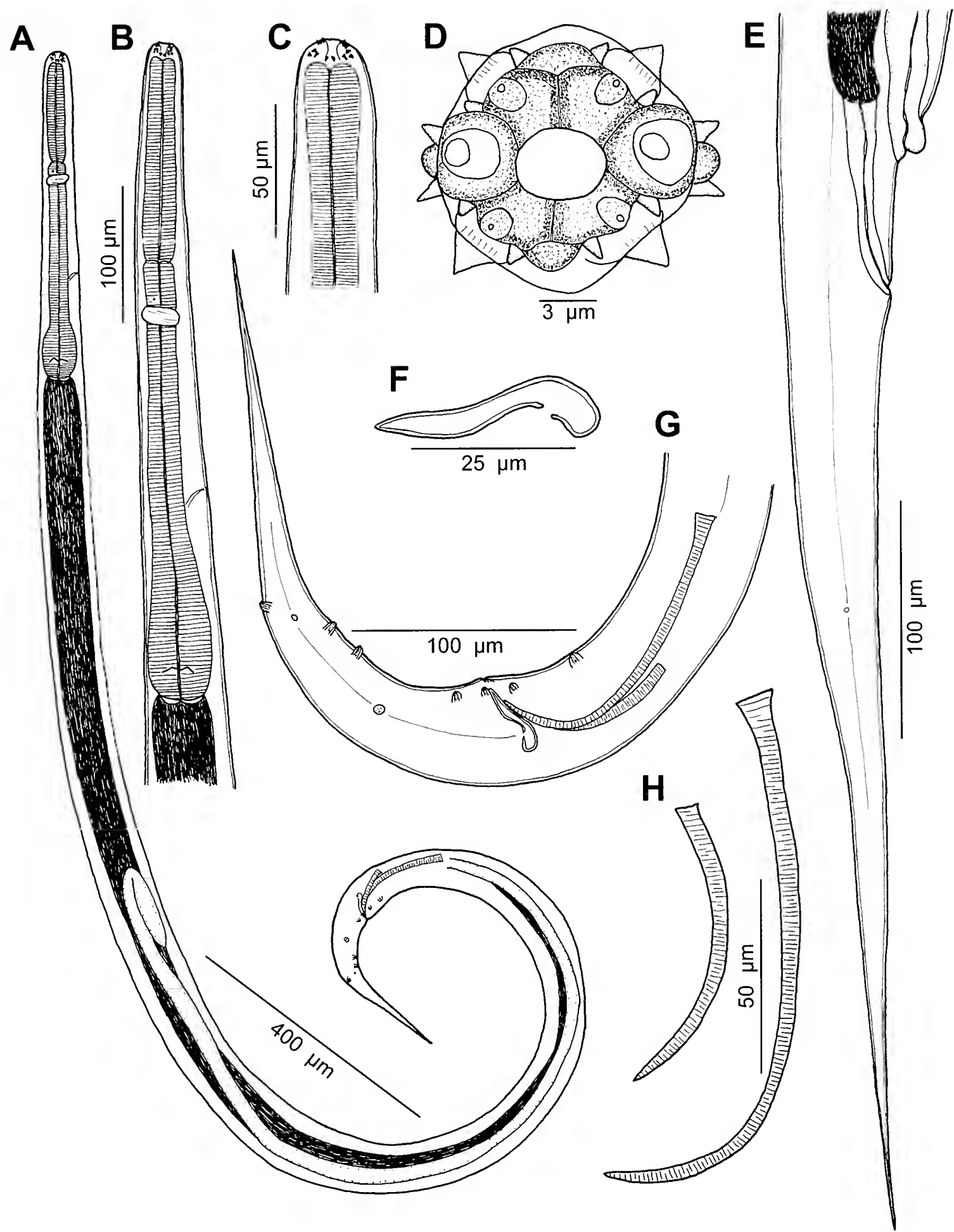


Fig. 1. *Orientattractis brycini* sp. nov. (A) Whole body of male, lateral view. (B, C) Anterior end of body, lateral views. (D) Cephalic end, apical view. (E) Posterior end of female, lateral view. (F) Gubernaculum, lateral view. (G) Posterior end of male, lateral view. (H) Spicules, lateral view.

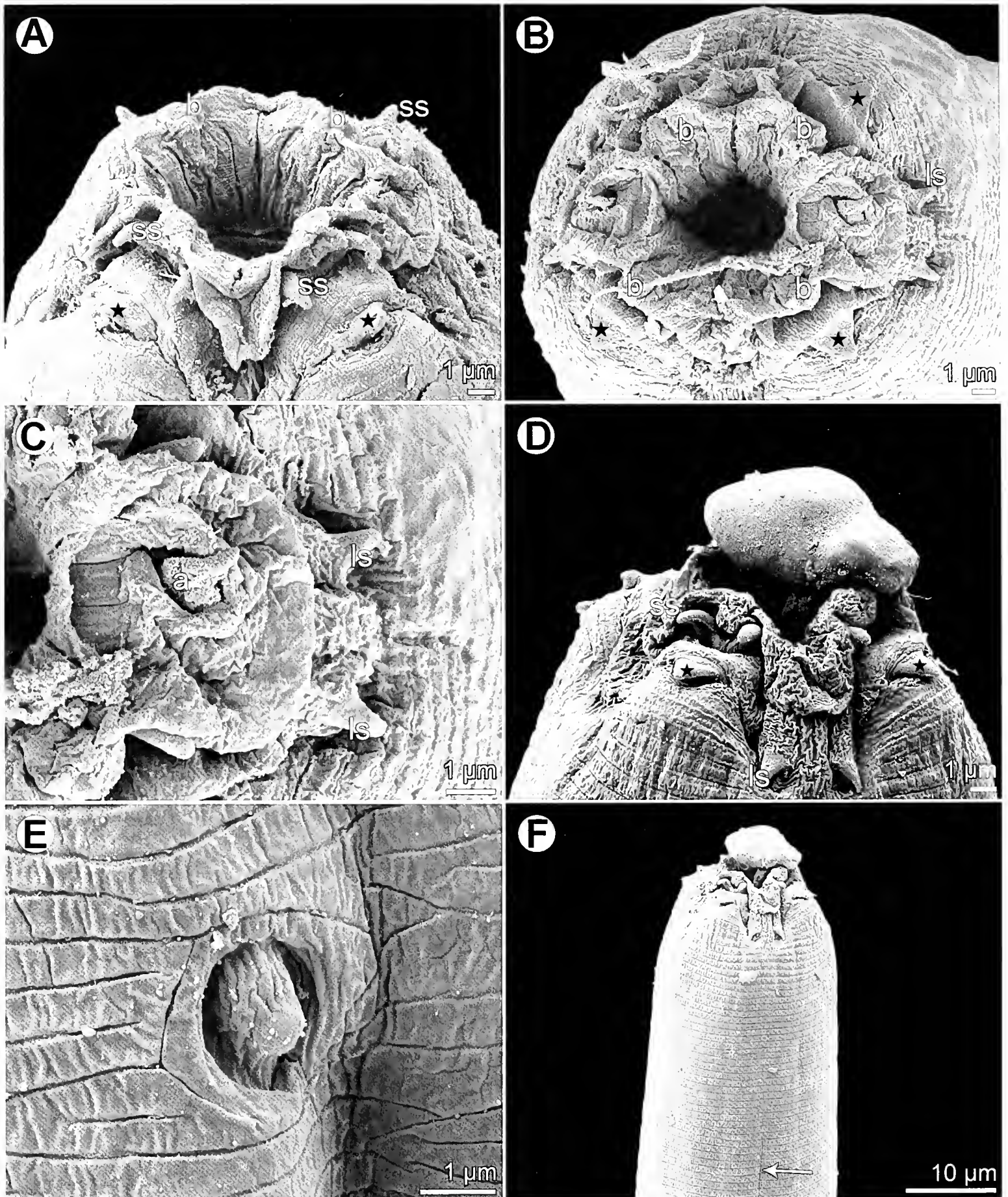


Fig. 2. *Orientatractis brycini* sp. nov., SEM micrographs. (A, B) Cephalic end, subapical and apical views, respectively (asterisks indicate single median spine). (C) Detail of lateral lip, amphid and lateral spines, apical view. (D) Cephalic end, sublateral view (asterisks indicate single median spine). (E) Deirid. (F) Anterior end of body (arrow indicates groove-like lateral ala). Abbreviations: a – amphid, b – cephalic submedian papilla, ls – lateral paired spine, ss – submedian paired spine.

one at same level and one posterior to it), 4 postcloacal pairs (first pair of postcloacals lateral, second and third pairs subventral and close to each other, fourth pair subdorsal) (Figs 1G, 3A). Pair of small, lateral outlets (probably representing phasmids) between pairs 3 and 4 of postcloacals (Fig. 3A, E). Single left-shifted papilla on anterior cloacal lip weakly-developed (Fig. 3C, D). Spicules unequal, similar, well-sclerotized. Left and right spicules 130-158 (148) and 75-90 (83) long, respectively. Both spicules with transverse striations along their lengths; proximal ends slightly expanded, distal ends sharply pointed (Fig. 1G, H). Gubernaculum 29-39 (37) long, well-sclerotized, proximal end rounded, with deep depression; distal end pointed and slightly ventrally curved (Fig. 1F). Tail 207-257 (229) long, with dorsal groove-like structure (Fig. 3B).

Female (13 gravid specimens; measurements of allotype in parentheses): Length of body 2.50-3.61 (3.30) mm, maximum width 60-129 (109). Length of corpus 126-170 (161), of isthmus 294-355 (318); entire esophagus 443-509 (479). Width of esophageal bulb 34-50 (43). Nerve ring, excretory pore, and deirids 158-221 (217), 292-347 (331), and 196-205 (-), respectively, from anterior end of body. Vulva with anterior lip slightly elevated, near the posterior end of body, 2.19-3.18 (2.91) mm from anterior end of body, somewhat anterior to anal opening (Figs 1E, 3F). Distance anus-vulva 39-72 (44). Vagina muscular, anteriorly directed. Uterus containing fully developed larvae 673-1176 (927) long; some females with developing eggs 236-305 × 93-110 (236-242 × 93-94). Tail 270-388 (348) long, with pore-like phasmids between first and second thirds of tail length (Fig. 1E).

Remarks

Petter (1966) erected the genus *Orientattractis* to allocate nematodes with a particular structure of the oral opening, specifically the presence of symmetrical groups of 3 sclerotized posteriorly directed spines surrounding mouth. Currently, this genus includes 7 valid species, namely: *O. asymmetrica* Gibbons & Platt, 2006 in *Rhinoclemmys pulcherrima* Gray (Testudines) from Costa Rica, *O. campechensis* González-Solís & Moravec, 2004 in *Paraneetroplus bifasciatus* (Steindachner) (reported as *Vieja bifasciata*) and *Cichlasoma pearsei* (Hubbs) (both Perciformes) from Southern Mexico, *O. chiapasensis* González-Solís & Moravec, 2004 in *Theraps intermedius* (Günther) (reported as *Vieja intermedia*) and *Tomocichla tuba* (Meek) (both Perciformes) from Southern Mexico, *O. hamabatrachos* Bursey, Goldberg & Kraus, 2014 in *Austrochaperina basipalmata* (van Kampen) (Anura) from New Guinea, *O. levanhoai* (type species) in *Indotestudo elongata* (Blyth) (reported as *Testudo elongata*) (Testudines) from Vietnam, *O. leiperi* Buckley, 1969 in *Podocnemis vogli* Müller (Testudines) from Colombia, and *O. mekongensis* Moravec, Kamchoo & Pachanawan, 2015 in *Pangasius bocourti* Sauvage (Siluriformes) from Thailand (Petter, 1966; Buckley,

1969; González-Solís & Moravec, 2004; Gibbons & Platt, 2006; Bursey *et al.*, 2014; Moravec *et al.*, 2015).

Even though the type species of the genus was not reviewed, we decided to emend the generic diagnosis, based on the already described species and present data, since several important features were not included in the original description (see Petter, 1966). Morphological features as the structure of the oral opening, presence of deirids, among others, were incorporated to the diagnosis for making it easier to distinguish *Orientattractis* from closely related genera (e.g., *Klossinemella* and *Paraorientattractis*) within the Atractidae. Thus, *Orientattractis* and *Paraorientattractis* have four bicornate submedian structures surrounding mouth, whereas *Klossinemella* shows eight pairs; the two first genera differ in the number of lips (6 vs. 4) and presence of ornamentations on the dorsal surface of body in *Paraorientattractis*. These changes do not modify the systematic position of the genus.

The four bicornate structures along with a pair of spines posterior to amphidial pore are only present in *O. brycini* sp. nov., *O. hamabatrachos*, and *O. leiperi*; while in *O. asymmetrica*, *O. campechensis*, *O. chiapasensis*, *O. levanhoai*, *O. mekongensis* are lacking.

Orientattractis brycini sp. nov. shows similar body length to that of *O. chiapasensis*, and is near the lower size range of *O. campechensis*, *O. leiperi* and *O. levanhoai*, whereas the remaining three species (*O. asymmetrica*, *O. hamabatrachos*, *O. mekongensis*) have larger bodies. However, *O. brycini* sp. nov. differs from all species within the genus in the size of both spicules (except in *O. hamabatrachos*), gubernaculum and number and distribution of caudal papillae (see Table 1).

The new species shares some similarities with *Paraorientattractis semiannulata* Gibbons, Khalil & Marinkelle, 1997, a nematode of *Podocnemis unifilis* Troschel (Testudines) in Brazil (Gibbons *et al.*, 1997). Both species harbour identical shape and structures surrounding mouth, such as each submedian lip with a pair of recurved pointed spines and single median spine near their distal margin, along with a pair of smaller spines posterior to amphidial pores. Moreover, both have two unequal, striated spicules, similar gubernaculum and number of caudal papillae. However, they differ in the ornamentations on the dorsal surface of body and striated, broad, well-developed lateral alae in *P. semiannulata*.

Caballero-Rodríguez (1971) described *Proattractis parvicapitricoronata* from the tortoise *Staurotypus triporcatus* in Veracruz, Mexico. Later, this species was transferred to *Klossinemella* as *K. parvicapitricoronata* by Moravec & Thatcher (1997). González-Solís & Moravec (2004) stated that it probably belongs to *Orientattractis* according to the shape of spicules, number and distribution of caudal papillae and structure of the anterior end, but until the type material of *K. parvitricoronata* is re-examined, it should be retained within the genus *Klossinemella*.

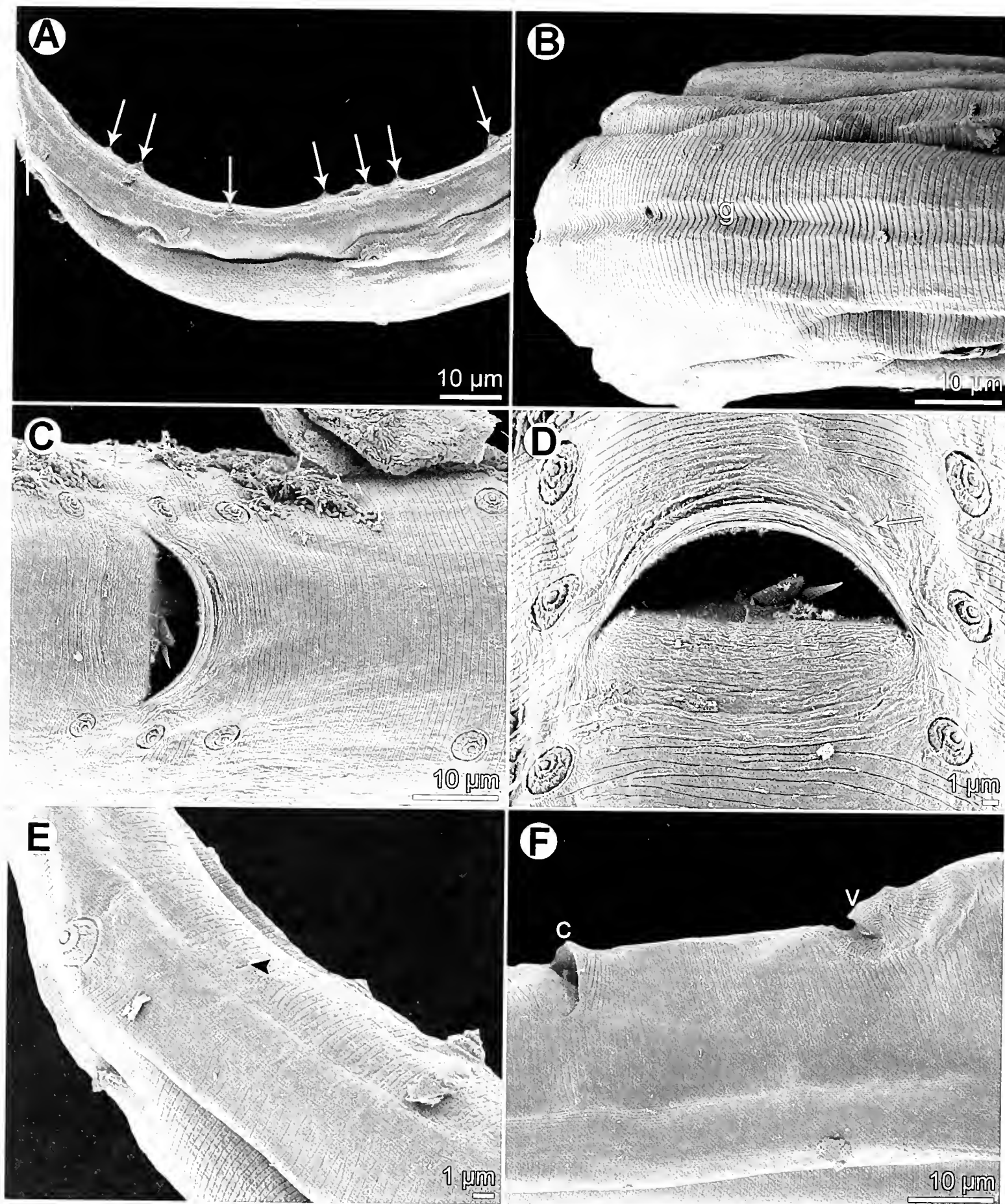


Fig. 3. *Orientatractis brycini* sp. nov., SEM micrographs. (A) Posterior end of male, sublateral view (arrows indicate caudal papillae). (B) Dorsal surface of male tail. (C, D) Region of cloaca, ventral views (arrow indicates left-shifted unpaired papilla). (E) Posterior end of male, lateral view (arrowhead indicates phasmids). (F) Region of anus and vulva, lateral view. Abbreviations: c – anus, g – groove-like dorsal structure, v – vulva.

Table 1. Comparison of some selected measurements of the valid species of *Orientattractis* around the world; measurements are in micrometers, unless otherwise stated.

	Body length (mm)		Spicule length		Gubernaculum length	Caudal papillae*
	male	female	right	left		
<i>O. asymmetrica</i>	4.1-4.3	3.7-5.5	86-104	220-239	56-66	4: 2: 3 + 1
<i>O. brycini</i> sp. nov.	2.6-3.1	2.5-3.6	75-90	130-158	29-39	1: 3: 4
<i>O. campechensis</i>	3.0-3.5	3.3-4.3	84-106	430-506	62-74	0: 5: 4 + 1
<i>O. chiapasensis</i>	2.7-3.0	2.0-3.8	60-68	204-238	44-49	0: 5: 4 + 1
<i>O. hamabatrachos</i>	3.2-4.3	3.4-4.9	79-98	146-165	55-67	2: 1: 5 + 1
<i>O. leiperi</i>	3.0-3.9	2.7-4.3	160	470	76	3: 1: 5 + 1
<i>O. levanhoai</i>	3.3	3.4	90	170	40	3: 0: 5
<i>O. mekongensis</i>	5.3-6.6	7.7-8.9	90-105	306-384	33-51	2: 1: 5

* pairs of caudal papillae (without considering phasmids): precloacal: adcloacal: postcloacal + single median papilla (left-shifted in *O. brycini* sp. nov.)

Interestingly, *O. brycini* sp. nov. was found in two fish species of the order Characiformes, but from different families (Alestidae and Distichodontidae) and sampling localities (Ogooue and Mpassa). Despite this, there were no differences in the morphology and biometrical values among the nematodes from both hosts, although certain morphometric variability always occurs intraspecifically. Such morphological and biometrical variability which might be associated with local ecological conditions and physiological traits of host species is not uncommon (see González-Solís & Moravec, 2004). Nothing is known about the life cycle of these nematodes, but as in other members of Atractidae, larvae develop to the third stage in uterus, thus auto-infection is possible (Anderson, 2000). Viviparity has greatly helped attractid nematodes to parasitize several unrelated vertebrates (i.e., turtles, fish, amphibians, grazing mammals) by venereal and oral transmission (Baker, 1982), and to be distributed in different zoogeographical regions (America and Indonesia). The present finding represents the eighth species in the genus *Orientattractis* and the fourth being reported from fish hosts, since other members were reported in tortoises (*O. levanhoai*, *O. leiperi*), frog (*O. hamabatrachos*), and turtle (*O. asymmetrica*). This is also the first record of a species of *Orientattractis* in Africa, which expands the geographical distribution of the genus, since it was previously reported from Costa Rica, Colombia, Mexico (American continent), Thailand, Vietnam (Southeastern Asia) and New Guinea (Melanesia).

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***Apharinodes sinensis* sp. n. (Coleoptera: Staphylinidae: Pselaphinae) from China, and discovery of male wing dimorphism in Hybocephalini**

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Abstract: *Apharinodes sinensis* sp. n. is described from Yunnan, and represents the first named species of the tribe Hybocephalini Raffray from China. Male wing dimorphism is for the first time reported for a hybocephaline. An identification key to the four known *Apharinodes* species is given.

Keywords: Hybocephalini, *Apharinodes*, taxonomy, new species, male wing dimorphism, Asia.

INTRODUCTION

The ant-loving beetle tribe Hybocephalini Raffray (Pselaphinae: Pselaphitae) comprises some 70 species grouped in 10 genera (Newton & Chandler, 1989; Besuchet 2008). Within this tribe most members are found from the tropical forested areas of Africa and Oriental region (Raffray, 1908; Newton & Chandler, 1989), with two species (of *Apharinodes* Raffray and *Stipesa* Sharp, respectively) occurring in eastern Palaearctic region (Sharp, 1874; Nomura, 1989), and one species (of *Stipesa*) from Australia (Chandler, 2001). Hybocephalines can be distinguished from those of all other tribes of the Pselaphitae by the generally compact and convex habitus, relatively robust antennae, small maxillary palpi, and more noticeably, squamous setae that may partially to entirely cover the body surface (Raffray, 1890a; Chandler, 2001). The number of the antennomeres by which the clubs are formed, relative length(s) of the abdominal segments, presence/absence and number of the abdominal paratergites, and presence/absence of elytral discal striae are frequently used to determine taxa at generic level (Raffray, 1908; Jeannel 1949a, b, 1959).

The genus *Apharinodes* Raffray is a small group currently including three species confined to East Asia (Raffray, 1911; Newton & Chandler, 1989; Nomura, 1989). Raffray (1890a) established *Apharinodes* with *A. squamosa* Raffray from Singapore (type species subsequently designated by Raffray, 1890b), and later described (Raffray, 1895) a second species *A. miranda* Raffray from the same country. Most recently, Nomura (1989)

described a third species *A. papageno* Nomura from Okinawa Island, Japan, from where additional collecting data for the same species was later added (Sugaya, 2003). The actual diversity of *Apharinodes* is expected to be much higher than currently documented. At least eight additional species from China, Malaysia and Thailand were listed in several reports on the local pselaphine fauna of these areas, though none of these has been formally named (Nomura 2000; Nomura & Idris, 2005; Nomura & Mohamed, 2008; Nomura *et al.*, 2008, 2010, 2013). *Apharinodes* has the antennal clubs composed of only the enlarged terminal antennomere (XI), the first two visible abdominal tergites (morphologically IV and V) are subequal in length, and almost the entire body surface is covered by thickened squamous setae. Such a combination of characters provides reliable means with regard to the identification of *Apharinodes* within the Hybocephalini.

Based on the third edition of the International Code of Zoological Nomenclature (ICZN, 1985), Nomura (1989) emended the gender of *Apharinodes* to masculine, and changed the suffixes of the two known species accordingly. But according to the latest (fourth) edition of the ICZN (1999), the name *Apharinodes* was originally combined with adjectival species-group names that are feminine (i.e. *squamosa* and *miranda*), thus the gender of *Apharinodes* should be remained as feminine (Article 30.1.4.4.).

Wing dimorphism is long- and well-known in insects. However, for the megadiverse polyphagan family Staphylinidae, sex-related wing dimorphism was only recently documented and discussed in detail. Thayer

(1992) firstly reported in *Omalius flavidum* Hamilton the presence of fully-winged and flightless males and flightless females, which belongs to a less common pattern of wing dimorphism. In Pselaphinae (formerly Pselaphidae, see Newton & Thayer, 1995), such pattern has been so far recorded for Batrisini (Nomura, 1991), Trichonychini (Nomura, 1988; Yin & Li, 2016), Bythinini (Kurbatov, 1994; Löbl *et al.*, 1998), and Tyrini (Nomura, 1997). In these groups, the males with normally developed hind wings tend to have larger eyes, longer elytra and metaventrite, and stronger elytral humeri. Recently, two male specimens of an undescribed *Apharinodes* were collected from southwestern China (Yunnan) exhibiting male wing dimorphism in a group of the Pselaphinae (Hybocephalini) in which such a phenomenon has never been recorded.

MATERIAL AND METHODS

Material studied in this paper is housed in the Insect Collection of Shanghai Normal University (SNUC).

Dissected parts were preserved in Euparal on plastic slides that were placed on the same pin with the specimen. The habitus image was taken using a Canon 5D Mark III camera in conjunction with a Canon MP-E 65 mm f/2.8 1-5X Macro Lens and a Canon MT-24EX Macro Twin Lite Flash. Images of the morphological details were made using a Canon G9 camera mounted on an Olympus CX31 microscope. Zerene Stacker (version 1.04) was used for image stacking. All images were modified and grouped in Adobe Photoshop CS5 Extended.

The label data of the material are quoted verbatim, with additional notes included in parentheses. The following abbreviations are applied: AL—length of the dorsally visible part of the abdomen (posterior to elytra) along the midline; AnL—length of the antenna; AnCL—length of the antennal club; AW—maximum width of the abdomen; EL—length of the elytra along the suture; EW—maximum width of the elytra; HL—length of the head from the anterior clypeal margin to the occipital constriction; HW—width of the head across eyes; PL—length of the pronotum along the midline; PW—maximal width of the pronotum. The length of the body (BL) is a combination of HL + PL + EL + AL. Terminology for morphological structures follows Chandler (2001) with the exception that the term ‘ventrite’ replaces ‘sternite’, except prosternum.

TAXONOMY

Apharinodes sinensis, new species

Figs 1-2

Type material: **Holotype:** macropterous male: ‘China: Yunnan Province, Lincang City, Yun Hsien (云县), Manwan Town (漫湾镇), Caozidicun (草子地村), 24°40’27”N, 100°23’09”E, under stone, 1757 m,

9.iv.2016, Zi-Chun Xiong leg.’ (SNUC). **Paratype:** 1 apterous male, same label data as the holotype (SNUC).

Diagnosis: BL 2.28-2.39 mm; postocular region longer than eye (Fig. 2A); anterolateral branches (Fig. 2A-1) of squamous scales on pronotum distinct but shorter than basolateral branches (Fig. 2A-2), basolateral branches and mediobasal branch (Fig. 2A-3) separated anteriorly; male antennomere XI with large, shallow semicircular excavation on mesal surface; aedeagus (Fig. 2G-H) weakly sclerotized, median lobe with large basal capsule, endophallus with three sclerites, parameres thick and short.

Description: *Macropterous male* (Fig. 1A). Body length 2.39 mm. Body light reddish brown, mouthparts and tarsi lighter in color (the light color of the two males available are possibly due to immature adult status); most part of dorsal surface covered with thick squamous setae.

Head (Fig. 2A) slightly longer than wide, HL 0.53 mm, HW 0.46 mm, small vertexal and frontal fovea largely covered by setae; eyes large, each composed of about 32 facets; postocular margins (Fig. 2B) longer than eyes, roundly narrowed toward head base; antennae (Fig. 2C) robust, scapes as long as combined length of next two antennomeres, antennomeres II transversely quadrate, III to X strongly transverse, successively wider, XI largest, mesal surface with large, shallow, semicircular excavation, AnL 0.95 mm, AnCL 0.33 mm, AnCL/AnL = 0.35; maxillary palpi small and short, three-segmented, with distinct conical palpal cone; gular area flat, densely covered with setae basolaterally.

Pronotum (Fig. 2A) slightly wider than long, PL 0.48 mm, PW 0.52 mm, lateral margins nearly straight at basal half, narrowed from middle toward apex; anterolateral branches of squamous scales distinct but short, extending less mesally than basolateral branches, mediobasal branch and basolateral branches clearly separated at anterior ends. Whole surface of prosternum (Fig. 2B) covered with dense setae.

Elytra convex, wider than long, EL 0.73 mm, EW 0.88 mm, posterior margin with band of dense setae; two basal foveae covered by squamous scales; with complete discal and sutural striae. Metathoracic wings fully developed. Mesoventrite densely covered with small squamous setae; metaventrite densely covered with setae at middle, areas posterior to mesocoxae with two elongate projections that extend to metaventral posterior margin.

Abdomen subglobose, wider than long, AL 0.65 mm, AW 0.86 mm; tergite IV (first visible tergite) as long as tergite V, with pair of lateral sulci, tergites VI and VII slightly shorter than V, VIII (Fig. 2D) circular viewed posteriorly; sternite IV (second visible sternite) to VII successively shorter, VIII (Fig. 2E) shallowly emarginate at middle, IX (Fig. 2F) well-sclerotized at apex, membranous at posterior half.

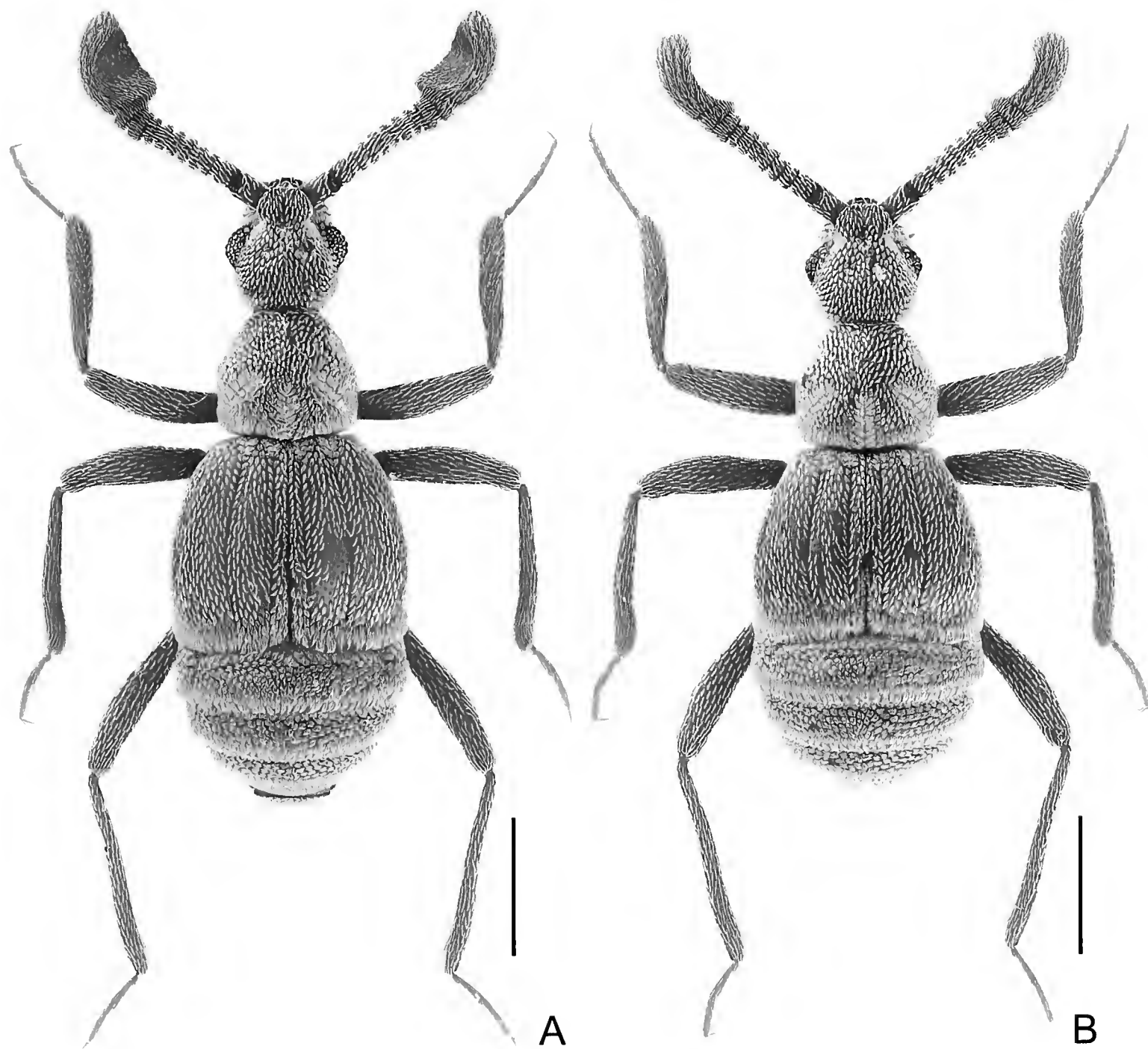


Fig. 1. Dorsal habitus of *Apharinodes sinensis*. (A) Macropterous male. (B) Apterous male. Scale bars: 0.5 mm.

Key to species of *Apharinodes* Raffray

- 1 Body less than 2 mm; anterolateral branches of squamous scales on pronotum extending more mesal (closer to midline) than basolateral branches. (Singapore) *A. squamosa* Raffray
- Body no less than 2 mm; anterolateral branches of squamous scales on pronotum shorter than basolateral branches (Figs 1, 3).....2
- 2 Male antennomere XI with large, shallow, quadrate excavation; pronotal mediobasal and basolateral branches of squamous scales fusing anteriorly (Fig. 3B). (Singapore)..... *A. miranda* Raffray
- Male antennomere XI with deep, rounded excavation (Figs 1, 2C, 3A); pronotal mediobasal and basolateral branches of squamous scales separated anteriorly (Figs 1, 2A, 3A)3
- 3 Excavation of male antennomere XI deeper (Fig. 3A); postocular margins slightly shorter than eye length (Nomura, 1989: fig. 1); pronotal anterolateral branches of squamous scales indistinct (Fig. 3A). (Japan: Okinawa)..... *A. papageno* Nomura
- Excavation of male antennomere XI shallower (Figs 1, 2C); postocular margins longer than eye length (Fig. 2A); pronotal anterolateral branches of squamous scales distinct (Figs 1, 2A). (China: Yunnan) *A. sinensis*, **sp. n.**

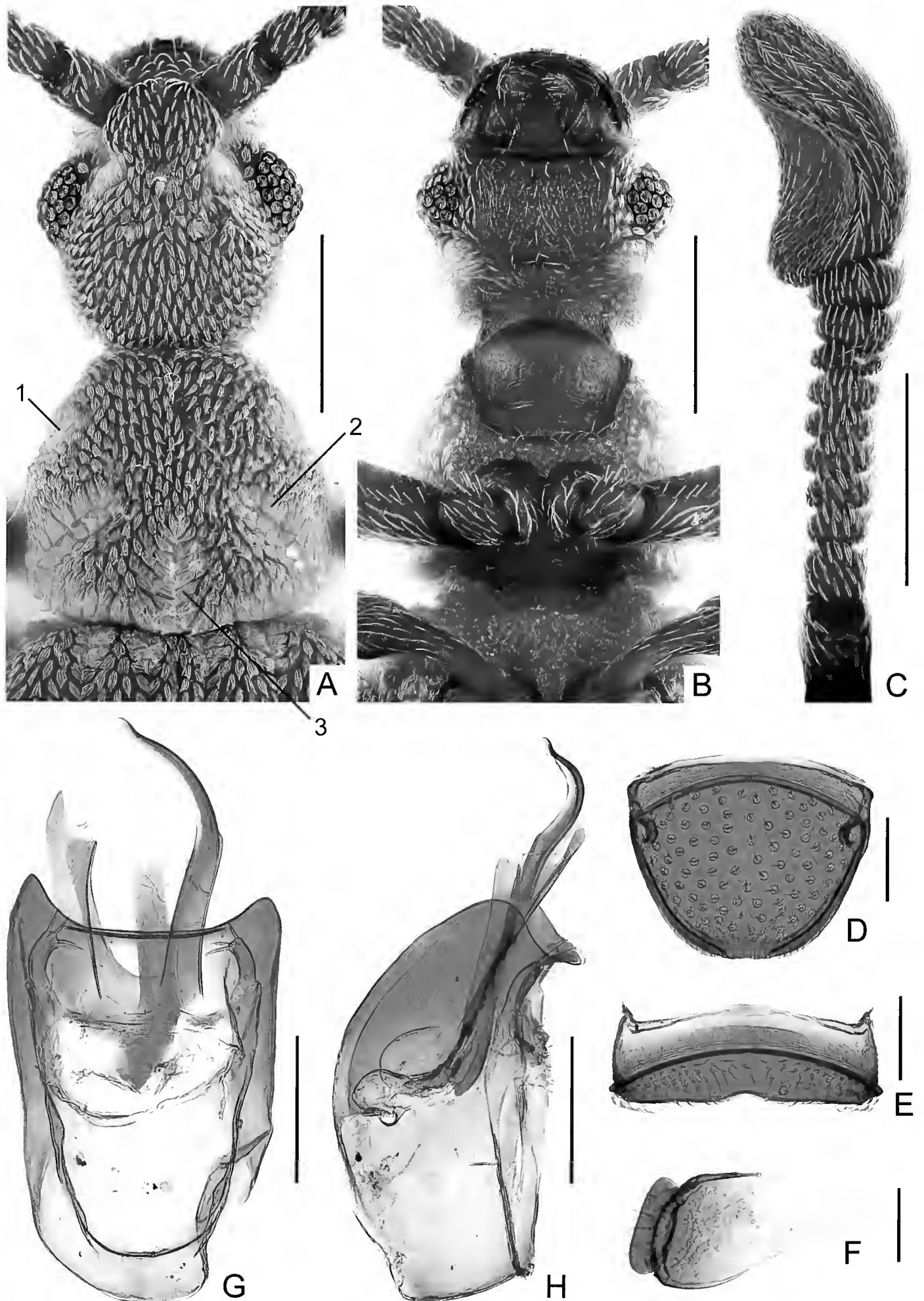


Fig. 2. Details of male *Apharinodes sinensis*. (A) Head dorsum and pronotum (numbers indicate branches of squamous scales: 1. anterolateral branch; 2. basolateral branch; 3. mediobasal branch). (B) Head venter and prosternum. (C) Right antenna. (D) Tergite VIII. (E) Sternite VIII. (F) Sternite IX. (G) Aedeagus, in ventral view. (H) Same, in lateral view. Scale bars: A-C = 0.3 mm; D, E, G, H = 0.1 mm; F = 0.05 mm.

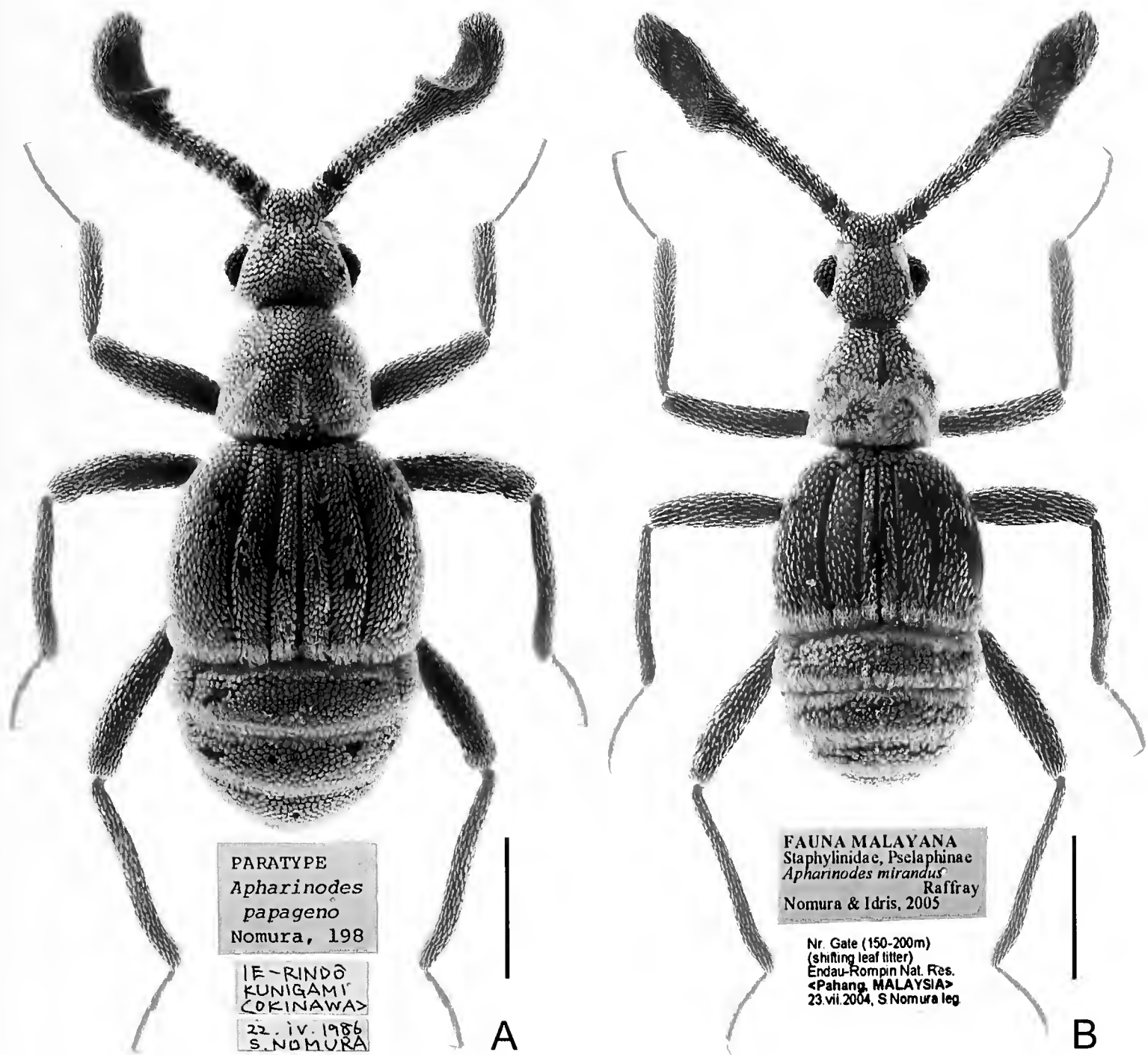


Fig. 3. Dorsal habitus of *Apharinodes* species. (A) *A. papageno*, male paratype. (B) *A. miranda*, male. Scale bars: 0.5 mm.

Aedeagus (Fig. 2G-H) weakly sclerotized, length 0.38 mm; median lobe broad, with large basal capsule, broadly emarginate along apical margin; parameres short and thick, each with three thick apical setae; endophallus composed of three sclerites, left sclerite longest, curved toward right, middle sclerite shortest, membranous, right sclerite broad, weakly sclerotized, narrowed at apex. *Apterous male* (Fig. 1B). Similar to macropterous male in general habitat, except eyes smaller, each composed of about 11 facets; elytra and metaventricle shorter; and metathoracic wings absent. Measurements: BL 2.28 mm, HL 0.50 mm, HW 0.44 mm, PL 0.47 mm, PW 0.52 mm, EL 0.65 mm, EW 0.87 mm, AL 0.66 mm, AW 0.85 mm,

AnL 0.97 mm, AnCL 0.34 mm, AnCL/AnL = 0.35, length of aedeagus 0.35 mm.
Female. Unknown.

Distribution: Southwestern China: Yunnan.

Etymology: The specific epithet indicating the country where the new species was collected.

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DNA barcoding of selected alpine beetles with focus on Curculionoidea (Coleoptera)

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Abstract: Selected beetles, mainly weevils, from the Alpine Arc were barcoded. From 187 samples of 106 assigned species of the families Curculionidae (152 samples, mainly Entiminae, Cyclominae and Hyperinae), Carabidae (18), Apionidae (6), Chrysomelidae and Staphylinidae (each 1 sample), sequences from the COI (subunit 1 of the cytochrome oxidase gene) were obtained, with a success of more than 86% (162 samples). In the cases of *Otiorhynchus pupillatus* Gyllenhal, 1834, *O. nodosus* (O. F. Müller, 1764), *O. meridionalis* Gyllenhal, 1834, *Dichotrachelus koziorowiczi* Desbrochers des Loges, 1873, *D. augusti* F. Solari, 1946 and *D. maculosus* Fairmaire, 1869 more diversity was hidden than foreseen in the beginning, suggesting partly cryptic (not yet described) species. One name is thus resurrected from junior synonymy (*O. civis* Stierlin, 1861 **stat. rev.** from synonymy with *O. meridionalis*). In another case with strictly parthenogenetically reproducing populations of *O. pupillatus* and *O. nodosus* in the Swiss Alps, several lineages from hypothetical postglacial immigration events, or alternatively complexes of species in *statu nascenti* might explain the results observed. Moreover, some morphologically debated species-pairs/triples confirmed to be problematic too, even with our COI sequence data [*Hypera nigrirostris* (Fabricius, 1775) – *ononidis* (Chevrolat, 1863) – *melarynychus* (Olivier, 1807)]. On the other hand, in some cases the species' identity, based on the monophyly of the investigated populations, could be confirmed [*Anthonomus rubi* (Herbst, 1795), *Polydrusus chaerodrysius* Gredler, 1866, *P. paradoxus* Stierlin, 1859]. In the hyperdiverse genus *Otiorhynchus* Germar, 1822, some preliminary insights into the systematics at the subgenus-level could be made, suggesting that many changes of the present morphologically based systematic structure will be necessary.

Keywords: COI - endemic species - Alps - Switzerland - Apionidae - Carabidae - Chrysomelidae - Curculionidae - Staphylinidae.

INTRODUCTION

Genetic analyses of speciation promises to substantially enhance our knowledge on evolution. In particular, the vast climatic oscillations during the present epoch of the quaternary can be linked closely to speciation processes and corresponding genetic change. Investigating the impact of the recent glacial periods has thus become a productive field in evolutionary research (Avise, 2000; Hewitt, 2004).

Of all extant taxa of higher living organisms, the Coleoptera are the most versatile, adaptive and successful group in exploiting ecological niches. Their success is reflected in persistence and adaptability of a huge variety of ancient lineages (Hunt *et al.*, 2007). Coleoptera are by far the most diverse group worldwide with about 400 000

described species (Hammond, 1992), thus representing one fourth of all animal taxa described. Since Hunt *et al.* (2007), a first comprehensive molecular phylogenetic reconstruction of the most diverse suborder Polyphaga exists.

In Switzerland, Coleoptera comprise more than 7000 species (estimation based on Besuchet, 1985). Whereas smaller families are less investigated, more than half of the species are covered presently by up-to-date checklists as Carabidae (Luka *et al.*, 2009a; 520 species); Staphylinidae (Luka *et al.*, 2009b; 1421 species); Curculionoidea (Germann, 2010a; 1070 species); Elateridae and allies (Chittaro & Blanc, 2012; 152 species); Cerambycidae, Buprestidae, Cetoniidae, Lucanidae (Monnerat *et al.*, 2015; 293 species), or are presently under investigation

(e.g. Chrysomeloidea, Cleridae, Histeridae and smaller xylobiont families). About 16 coleopterists are currently working on the mentioned families in Switzerland, the vast majority employing morphological approaches only. Alpine beetles have traditionally been regarded as a model group for the elucidation of the history of dispersal and formation of species. Of outstanding interest have been the immobile, flightless and endemic species currently inhabiting the highest ranges of the Alps and other mountainous regions. A century of classical zoological research has delivered quite a comprehensive knowledge on the alpine beetle fauna, and how it was formed through the “ice age” (Holdhaus, 1954; Janetschek, 1956). A recent study employing genetic analysis of carabid beetles could confirm the hypothesis of immobile alpine beetle species having a complex phylogenetic history, and also was able to address more general phylogeographic questions concerning the location of glacial refugia in the southern Alps (Lohse *et al.*, 2011).

The Superfamily Curculionoidea comprises globally more than 62 000 species (Oberprieler *et al.*, 2007), and hence form a superdiverse group within Coleoptera. Several attempts to unravel and explain the triggers for this diversity were made, either based on combined molecular and morphological data (Farrell, 1998; Wink *et al.*, 1997; Marvaldi *et al.*, 2002) or solely on molecular data using several genetic markers (McKenna *et al.*, 2009; Hundsdoerfer *et al.*, 2009). However, as Franz & Engel (2010) criticised, the results obtained by attempts of reconstruction of “big” phylogenies within Curculionoidea are ambiguous and inconsistent, and interpretations are built on weak grounds. More fruitful would be to address more specific questions, or questions concerning the classification at the genus, tribal or subfamily levels (Franz & Engel, 2010). Just very recently Haran *et al.* (2013) addressed such a question with the aid of next generation sequencing and provided well-supported new insights into weevil systematics at the subfamily level. Based on several traditional genetic markers, Astrin & Stüben (2008, 2010), Astrin *et al.* (2012) and Stüben *et al.* (2013) contributed substantially to the phylogenetic understanding within the subfamily Cryptorhynchinae, and Meregalli *et al.* (2013) investigated several Cyclominae. Similar promising insights could be done with other groups, where unresolved systematic questions at the genus and/or species level persist, as for e.g. Entiminae and Hyperinae, with many species living in restricted areas at higher altitudes.

In this study, we focus above all on relict populations of rare Alpine endemic (or potentially endemic) beetle species of the family Curculionidae and Carabidae with a particular interest in detecting possible cryptic diversity.

MATERIAL & METHODS

Taxon sampling

The present project includes 187 samples (see annex 1) belonging to more than 20 genera and representing about 100 recognised species of the families Curculionidae (representing 85% of all the samples used here), Carabidae (10%), Chrysomelidae, Apionidae, and Staphylinidae.

We are aware that many COI sequences of Coleoptera, including the families analysed here, are already available in a databank such as BOLD or GenBank. However, in the view of the extremely high number of existing sequences, we deliberately decided to confine our analysis to the Swiss alpine region, where samples are presently largely missing. Subsequent analyses, focusing on particular genera and subfamilies, will include all the needed sequence data to address the problem more in detail.

Before and after DNA extraction, all samples were and are stored in 90% Ethanol at minus 20°C and housed in the collection of the Nature-Museum Lucerne (NML). The extracted DNA is stored at minus 80°C and is currently deposited in the SwissBOL molecular platform at the University of Geneva.

DNA extraction, amplification and sequencing

Total genomic DNA was extracted using the DNeasy® Blood & Tissue Kit (Qiagen). Individuals were entirely plunged in the digestion buffer for 4 hours and removed thereafter. This technique allows a DNA extraction which preserves the exoskeleton and is useful when the specimen must be kept intact. Remaining protocols followed the supplier's instructions. Part of the mitochondrial COX1 (COI) gene was then amplified using the forward primer C1-J-2183 5'CAACATTTATTTTGATTTTTTGG3' and the reverse primer TL2-N-3014 5'TCCAATGCACTAATCTGCCATATTA3' (Vahtera & Muona, 2006). PCRs were made in 20 µl total volume with 0.60U Taq (Roche), 2 µl of the 10X buffer containing 20 mM MgCl₂, 0.8 µl of each primer (10 mM), 0.4 µl of a mix containing 10 mM of each dNTP (Roche) and 0.8 µl template DNA of unknown concentration. The PCR program comprised an initial denaturation at 95°C for 5 min, followed by 35 cycles of 95°C for 40 s, annealing at 42°C for 45 s and 72°C for 1 min, with a final elongation step at 72°C for 8 min. COI PCR products were then directly sequenced bi-directionally on an ABI 3031 automated sequencer (Applied Biosystems) using the same primers and following the manufacturer's protocol.

DNA sequence alignment and phylogenetic analyses

Sequence editing and generation of consensus sequences were accomplished using CodonCode Aligner (CodonCode Corporation). Alignments were automatically generated using Muscle (Edgar, 2004) as

implemented in Seaview program (Gouy *et al.*, 2010) and verified manually. Alternatively, the COI sequences were also edited with the Lasergene program Editseq (DNASTar Inc., Madison, WI, USA). Alignment of gene sequences was performed using the ClustalW method as implemented in Megalign (DNASTar Inc.) with default multiple alignment parameters. The COI alignment was gap free. ForCon (Raes & Van de Peer, 1999), a software tool for the format conversion of sequence alignments, was further applied. Phylogenetic and molecular evolutionary analyses were conducted using MEGA (Molecular Evolutionary Genetics Analysis) version 6 (Tamura *et al.*, 2013). Phylogenetic trees were obtained by applying the neighbour-joining (NJ) tree reconstruction method with Kimura 2-parameters (K2) as nucleotide substitution model and by using the Maximum Likelihood (ML) method based on the models selected by MEGA (i. e. GTR+I+G for the “Curculionoidea & Chrysomelidae” and Tamura-Nei+G for the “Carabidae & Staphylinidae”). To avoid misleading results when all data is combined in a single tree due to the lack of resolving power of the COI at higher systematic levels, we split the analyses in the two mentioned parts. The robustness of internal branches was assessed by bootstrapping. MEGA was also used for the visualisation and managing of the electropherograms and to calculate the genetic distances. The sequences of the gene analysed here have been deposited in BOLD (annex 1).

The results of the NJ tree are not depicted here, but they are available as electronically archived supplementary material (see Supp. 1 and Supp. 2 at the end of this publication).

RESULTS & DISCUSSION

Out of 187 extracted samples, 162 (more than 86%) could be used successfully to produce good and usable COI sequences (with an expected length of about 800 nucleotides). The by far biggest set of samples are from the weevils in the narrower sense, Curculionidae, with 152 samples of species from the subfamilies Entiminae (77 samples assigned to 43 described species), Hyperinae (23 samples assigned to 16 species), Cyclominae (27 samples assigned to 9 species), Curculioninae (7 samples assigned to 4 species) and Cryptorhynchinae (1 sample and species) in mostly several specimens from different populations. Six samples of Apionidae (genera *Aizobius*, *Hemitrichapion*, and *Osellaus*), which are part of the weevils in the broader sense, were included. Furthermore 18 Carabidae and one sample each of Chrysomelidae and Staphylinidae were included as well. Phylogenetic relationships obtained by both ML and NJ methods are depicted in Figs 1-2, resp. Supp. 1-2. The overall topology of the obtained trees is very similar (Fig. 1 vs Supp. 1 and Fig. 2 vs Supp. 2, respectively). In particular, the groups recorded in one analysis are identified in the

tree generated by using the other tree reconstructing method as well, however with variable bootstrap support (see below). The following discoveries could be made, reported under the respective systematic groups.

Family Apionidae Schönherr, 1823 **Genera *Aizobius* Alonso-Zarazaga, 1990** ***Hemitrichapion* Voss, 1859 &** ***Osellaus* Alonso-Zarazaga, 1990**

The Apionidae group is only weakly (NJ) or insufficiently (ML < 50%) supported in our analyses (Fig. 1, Supp. 1) but, on the contrary, the monophyly of the genera (i. e. *Aizobius*, *Hemitrichapion*, and *Osellaus*) found strong support in both the ML and NJ tree.

The genus *Osellaus* is represented with three strictly subalpine-alpine taxa in the western alpine arch – *O. bonvouloirii baldensis* (Bellò, Meregalli & Osella, 1980) on Monte Baldo, *O. bonvouloirii* s. str. (Ch. Brisout, 1880) in the central and western Alps and *O. bonvouloirii occidentalis* Germann, 2010 in the Vercors (Germann & Szallies, 2011). We included three Swiss populations of the nominal subspecies, but the third one from the Valais did not produce a positive PCR. The one from Uri (Brisen) and the other from Fribourg (Kaiseregg) are from localities just 91 km distant from each other. As *O. bonvouloirii* is a flightless, and restricted to its alpine habitat and thus a very low mobile species, the detected differences (K2 distance: 0.059; Table 1) are well explainable.

Three other Apionidae were included, of which *Mesotrichapion punctirostre* (Gyllenhal, 1839) did not give a result. The species with the widest distribution reaching from Central Asia to France is *Aizobius sedi* (Germar, 1818). However, the species is restricted to xerothermic places and unable to fly, this may explain for the rather large intraspecific genetic distance (0.027) between the two samples taken 300 km from each other. The third species sampled is *Hemitrichapion waltoni* (Stephens, 1839), recorded from Hungaria to France. The samples taken at localities separated by a distance of 340 km, a species which has normally developed hind wings and is the most mobile of all species included and may therefore show the lowest genetic distance of all Apionidae included (0.011).

These results underline once more the importance of the need for conservation of isolated populations of flightless, ecologically highly specialised and thus low mobile endemic species.

Family Curculionidae Latreille, 1802 **Subfamily Curculioninae Latreille, 1802** **Genus *Anthonomus* Germar, 1817**

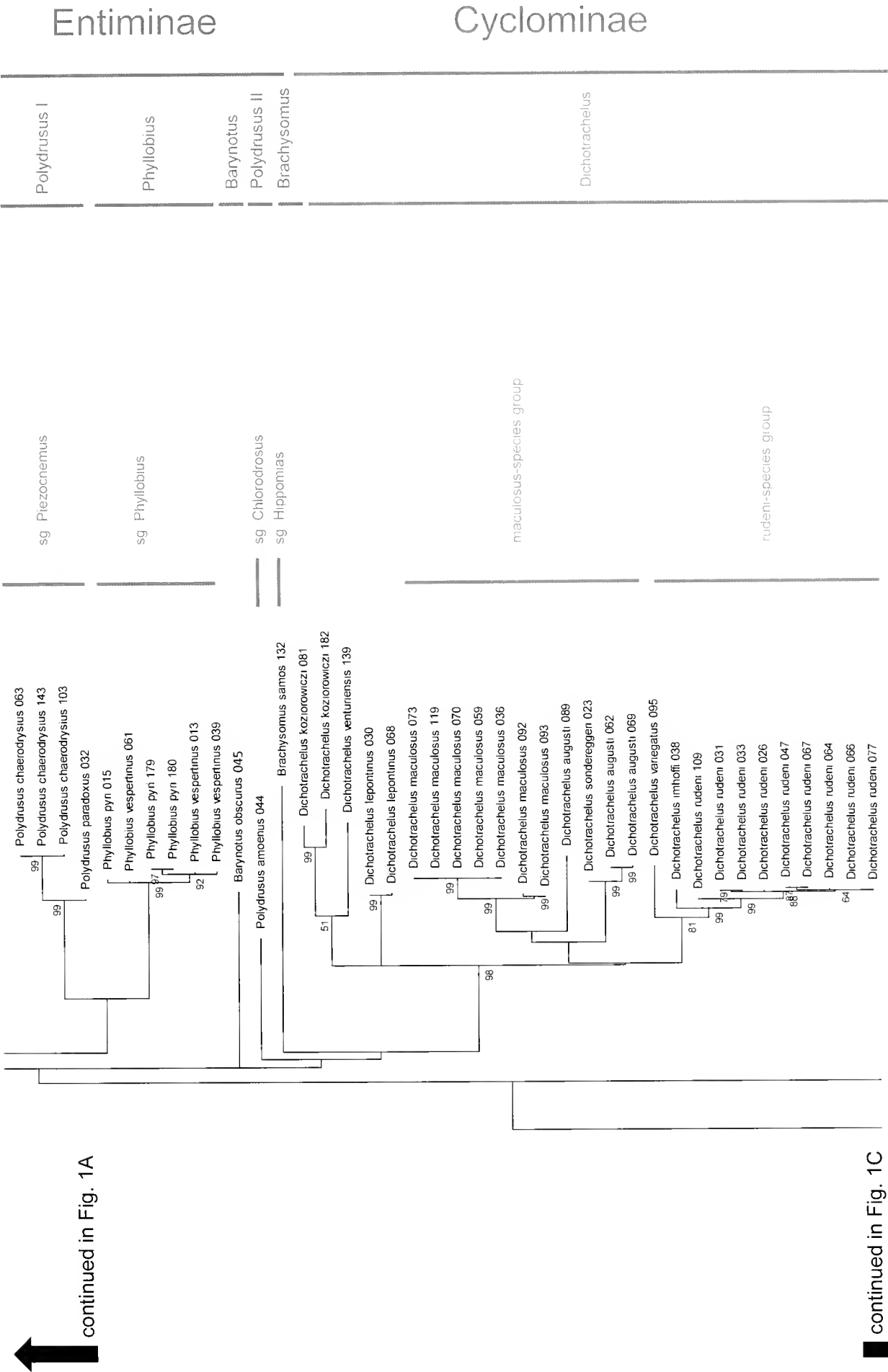
The samples of the genus *Anthonomus* form a strongly supported monophyletic group in both our analyses

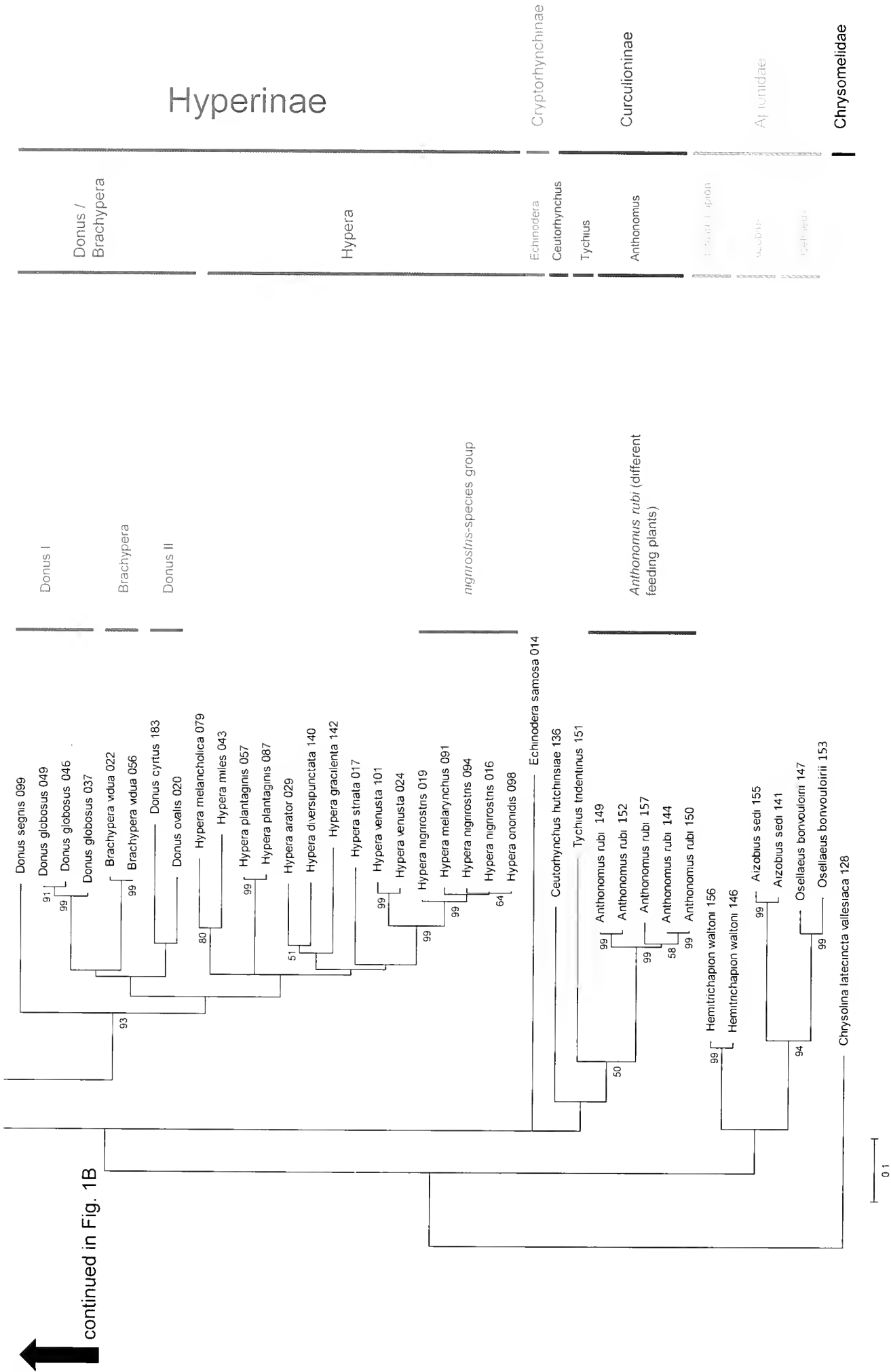
Entiminae

Otorhynchus



Fig. 1. Best Maximum Likelihood tree (-ln=13697.7060; GTR+I+G model as selected by MEGA) based on COI sequences of 142 samples of Curculionoidea (Apionidae and Curculionidae) and Chrysomelidae obtained by using MEGA 6. Values (over 50%) of bootstrap support from 100 pseudo-replicates are depicted above nodes.





(Fig. 1, Supp. 1). The Swiss populations of the species-pair *Anthonomus rubi* (Herbst, 1795) / *brunnipennis* Curtis, 1840 were investigated. There is some ambiguity about the status of *A. brunnipennis* in the Alps. The species shows a supposedly boreoalpine distribution (Germann, 2010b) and lives on *Dryas octopetala*, a boreoalpine cushion plant, and in northern Europe it lives also on *Filipendula ulmaria* L., *Potentilla palustris* L. and *P. erecta* L. *Anthonomus rubi* on the other side is a widespread species living on different Rosaceae, but also Cistaceae. Both species are very difficult to separate based on morphological traits, which overlap largely. The finds of *brunnipennis* from Switzerland were preliminarily termed as somewhat doubtful and a molecular re-investigation was suggested (Germann, 2010b, 2011a).

We here included a heterogeneous set of samples collected from the northern Alps, from Grisons and Ticino, and collected from either *Dryas octopetala* (sample 150 from Grisons; sample 144 northern Alps) being small and brownish and thus corresponding to *A. brunnipennis*, and from *Helianthemum* and *Potentilla* (sample 157 from nearby Italy and sample 152 from the northern Alps) being bigger and black and corresponding to typical *A. rubi*. However, the investigated COI sequences do not support the hypothesis that the specimens collected from *Dryas octopetala* are a sister-clade to the remaining supposedly „true“ *Anthonomus rubi* (highest intraspecific variability of 0.046; range 0.002-0.046). This might indicate that *A. brunnipennis* does not occur in Switzerland, however this should be corroborated with specimens of typical *A. brunnipennis* from northern Europe. On the other hand, an incomplete lineage sorting and/or a too short speciation time being detected by our COI barcode marker might explain our outcome (see also the discussion about the *Hypera nigrirostris*-group below).

Family Curculionidae Latreille, 1802
Subfamily Cyclominae Schönherr, 1826
Genus *Dichotrachelus* Stierlin, 1853

The monophyly of the genus *Dichotrachelus* is strongly supported in both our analyses (Fig. 1, Supp. 1). Within this genus, there is definitely more hidden diversity in these relatively immobile typically alpine living species distributed from the Rif Mountains of Morocco to the Carpathians in the east, with a speciation centre in the arc of the Alps. The species are ecologically bound either to mosses (“old” lineages) or Saxifragaceae (“derived” lineages) (Meregalli *et al.*, 2015). Based on COI sequences, we found at least in three species considerable differences among the samples, promoting the hypotheses of existing cryptic species.

Data from *D. koziorowiczii* Desbrochers des Loges, 1873 from two localities on Corsica (one in the North at Col de Verghio; the other in the South on Monte Calva) show

that two taxa (K2 distance: 0.067; Table 2) are likely to occur on this island, instead of one at present described species. Only the examination of the type specimen(s) will help to resolve this issue, as no precise type locality on the island has been given by Desbrochers (1873).

Similarly, with the *D. maculosus* Fairmaire, 1869 -species group, where specimens of *D. maculosus* from rather isolated populations in the Vercors, at the western border of the main distribution area, differ from those from the Swiss Prealps (K2 distance: 0.026).

Also in the *D. augusti* F. Solari, 1946 -species complex, more morphological diversity was discovered (see Germann, 2011b), here corroborated partly by the detected genetic diversity. The rather isolated population from the Saas Valley (sample 89) differs genetically considerably (K2 distance: 0.115!) from those of samples from the Grand St. Bernard and Col de Balme regions at the Swiss-Italian and Swiss-French border, which is indeed surprising, as it is surprisingly not reflected in their morphology, whereas *D. sondergeri* Germann, 2011 shows differences, but solely results in a genetic distance of 0.016 compared with the western populations of *D. augusti*. Furthermore, the different forms of the penis (Germann, 2011b) detected in the western populations of *D. augusti* in turn are not supported by relevant differences in the COI (0.002). However, to definitely delimit and show more solid insights into the systematics of the *D. augusti*-species complex we would still have to include samples from the type locality of *D. augusti* from around Champoluc in Valle d’Aosta. Additionally, the highly specialised habitat demands of the *D. augusti*-species complex might explain for the genetic differences between geographically close populations: all species of this complex live in mosses growing in alpine scree slopes, an unusual and certainly underestimated habitat, less in Carabidae (where exciting discoveries have been reported e.g. Molenda, 1996; Molenda & Gude, 2003; Huber & Molenda, 2004), or Staphylinidae (Molenda, 1999), but more in weevils where hardly any research has been done, and a promising field for investigations lies idle (Nikolai Yunakov, personal comm.). The alpine scree slopes thereafter can be seen as islands for the populations of the *D. augusti*-complex, where gene exchange via migrating individuals across alpine grasslands and glaciers might be very limited. This specific case once more shows that samples from populations of a species, at least if we deal with low mobile species, should be chosen very carefully.

The samples of species assigned to the *D. rudeni*-species group, based on a similar external morphology and male genitalia with a prolonged, laterally flattened tip of penis, also clustered together (*D. rudeni* Stierlin, 1853, *D. imhoffi* Stierlin, 1857 and *D. variegatus* Daniel & Daniel, 1898) and therefore support the outcomes from previous morphological investigations (Table 2). The samples of *D. rudeni* cluster all together with high bootstrap support (ML 99%, respectively NJ 98%),

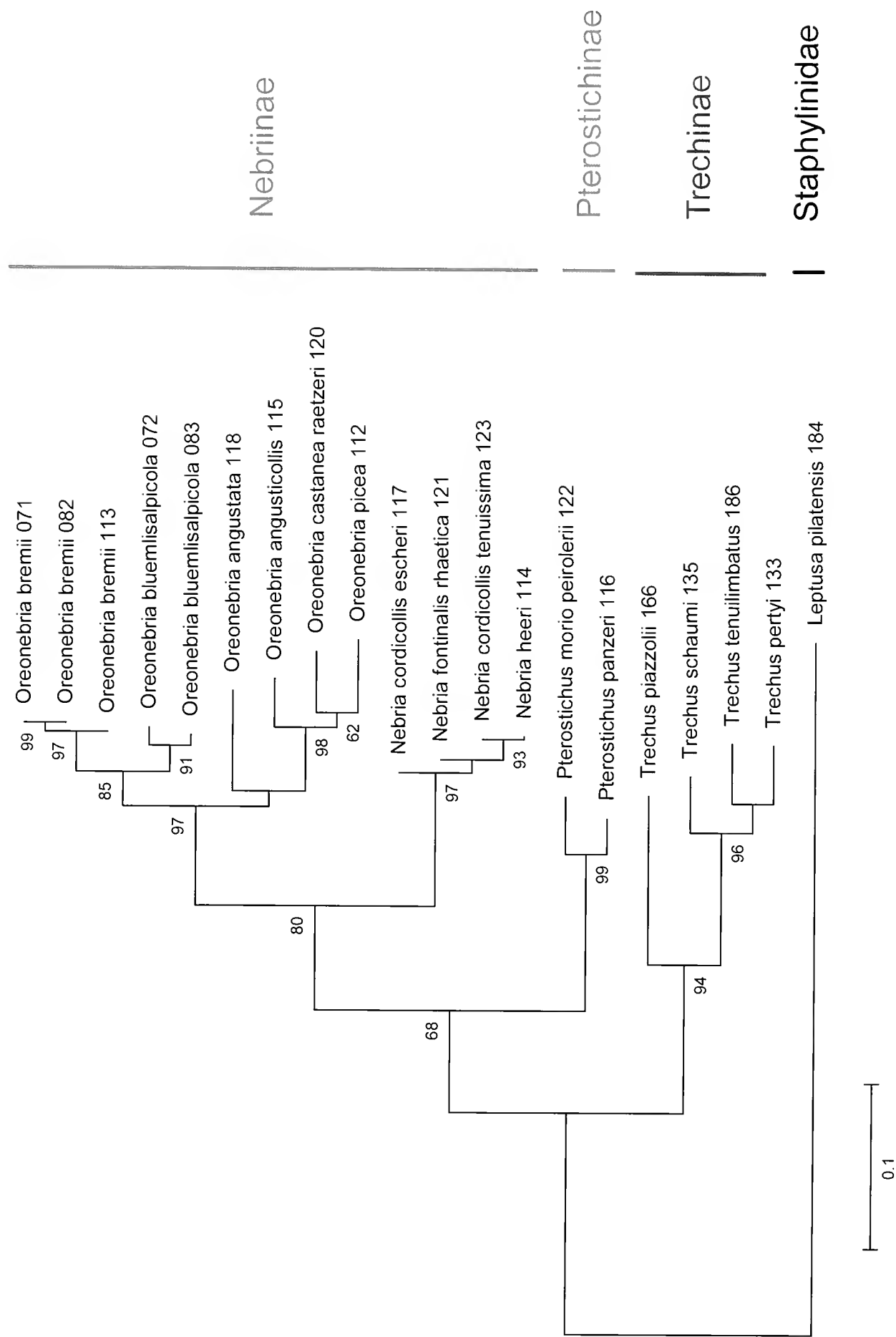


Fig. 2. Best Maximum Likelihood tree (-ln= 3045.2577; Tamura-Nei+G model as selected by MEGA) based on COI sequences of 20 samples of Carabidae and Staphylinidae obtained by using MEGA 6. Values (over 50%) of bootstrap support from 500 pseudo replicates are depicted above nodes.

although there is some herogeneity in it with sample 109 from the eastern border of the distribution near Disentis (sample 109) differing most from the others (0.010 to 0.016).

Family Curculionidae Latreille, 1802
Subfamily Hyperinae Lacordaire, 1863
Genera *Brachypera* Capiomont, 1868 and
***Donus* Jekel, 1865**

The genera *Brachypera*, *Donus* and *Hypera* form a strongly supported monophyletic group in both our analyses (Fig. 1, Supp. 1), with both individuals of *Brachypera vidua* (Gené, 1837) placed within *Donus* samples, even if with insufficient bootstrap support (<50%).

Despite of recent efforts to unravel the relationships at genus-level based on morphology within Hyperini (Skuhrovec, 2013), we recovered an alternative hypothesis regarding *Donus* and *Brachypera*; where the latter at best represents a subgenus within *Donus*. Although, in our dataset *Brachypera* is solely represented by *Brachypera vidua*. However, these results are supported by those of Stüben *et al.* (2015), who included *Brachypera grandini* (Capiomont, 1868), *B. dauci* (Olivier, 1807) and *B. lunata* Wollaston, 1854, which clustered also paraphyletically in different clades within *Donus*. In our analyses, the bootstrap support for two separate clades (*Donus* s. l. vs *Hypera*) is surprisingly low and their monophyly could not be therefore definitively established based on our sequence data.

Genus *Hypera* Germar, 1817

Even at the species-level, we found no support for a monophyly of all the *Hypera* species investigated here based on our COI data (Fig. 1, Supp. 1). In particular, the recorded genetic distances (Table 3) were relatively low (from 0.003 to 0.012) for any of the three species of the *H. nigrirostris* group [*nigrirostris* (Fabricius, 1775), *ononidis* (Chevrolat, 1863) and *melarynchus* (Olivier, 1807)]. The morphologically weakly supported hypothesis of the species status for *Hypera ononidis* was already questioned by Stüben *et al.* (2015) in their barcode approach. Although, obvious ecological differences are evident (*H. ononidis* lives on *Ononis* spp. and occurs in a sub-area of *H. nigrirostris*, which accepts a wider range of Fabaceae). Therefore, a more recent speciation process (not yet detectable with the possibly too conservative COI-marker), and thus the evolution of eco-species at an early stage of differentiation might be an explanation for this circumstance. Interestingly also the morphologically close *H. melarynchus* – living on the Fabaceae *Ononis ramosissima* – clustered together with *H. ononidis* + *nigrirostris*. However, *H. melarynchus* shows several morphological characters (biggest species

of all three > 5 mm; rostrum long and slender, at least as long as pronotum; 7th article about as wide as club; elongate elytra parallel along middle; penis S-shaped in lateral view, tip elongate, tongue-like) that allow an unambiguous separation from *H. nigrirostris* and *H. ononidis*, and therefore the species status has never been questioned. This provides further evidence that the *nigrirostris*-species group might indeed represent a younger group where speciation is at an early stage with an incomplete lineage sorting and highlighting therefore the limited resolution power of the used barcoding marker (see Germann *et al.*, 2010 for a similar case in Diptera).

Family Curculionidae Latreille, 1802
Subfamily Entiminae Schönherr, 1823
Genus *Otiorhynchus* Germar, 1822
Subgenera *Metopiorrhynchus* Reitter, 1912 pars,
***Nihus* Reitter, 1912, *Eunihus* Reitter, 1912**

A large number of the specimens coped with this study belongs to the genus *Otiorhynchus* (annex 1, Fig. 1, Supp. 1). This genus is one of the most specious genera – if not the most specious – in weevils. More than 1500 species are presently assigned to this genus and the systematics is midly expressed rather chaotic. Based on our data, the monophyly of *Otiorhynchus* is supported by insufficient bootstrap values in both the NJ and ML analyses. However, some new insights into alpine subgenera could be gained even if the overall relationships among all the proposed subgenera within this large genus are not always strongly supported in our analyses based on a relatively short fragment of the COI gene.

It was Yunakov (2006) who proposed subgenus *Metopiorrhynchus* as synonym to *Nihus* Reitter, 1912, which was reinstated by Magnano & Alonso-Zarazaga (2013). [The type species of *Metopiorrhynchus* is *O. singularis* (Linné, 1767) – included in our samples, and *O. carinatopunctatus* in *Nihus*, a sample that remained negative] We here provide support to the former synonymy, where species of *Nihus* cluster together within the subgenus *Metopiorrhynchus*. Interestingly, the only representative (*O. grischunensis* Germann, 2010) of *Eunihus*, a subgenus which has temporarily been placed in synonymy with *Nihus*, but is actually accepted as proper subgenus (Magnano & Alonso-Zarazaga, 2013), does not cluster together with *Nihus*. Even if the position of *Eunihus* remains unclear since not supported by enough bootstrap values, our result underlines its self-standing position in relation to the typical *Nihus* representatives. On the other side, the Corsican endemic species (*O. corsicus* Fairmaire, 1859) at present assigned to the subgenus *Phalantorrhynchus* Reitter, 1912 results in the clade *Metopiorrhynchus* + *Nihus* (bootstrap support ML: 58; NJ: 61).

Schütte *et al.* (2013) and Stüben *et al.* (2015) already provided molecular evidence to a common clade of

Nihus + *Metopiorrhynchus* + *Aranihus* Reitter, 1912 [represented by the species *O. parvicollis* Gyllenhal, 1834 and *O. ligneus* (Olivier, 1807)] + *Edelengus* Reitter, 1912 (*O. atlasticus* Escalera, 1914; *O. allardi* Stierlin, 1872).

Genus *Otiorhynchus* Germar, 1822

Subgenera *Metopiorrhynchus* Reitter, 1912 pars and *Postaremus* Reitter, 1912

In all our analyses (Fig. 1, Supp. 1), all the samples belonging to *Otiorhynchus pupillatus* Gyllenhal, 1834 clustered together with high bootstrap support. *Otiorhynchus pupillatus* is a highly polymorphic species. It varies in many characters as size, proportions (rostrum, pronotum and elytra), vestiture (e.g. form of scales, density), size of teeth on femora, and (female) genital organs. It reproduces almost strictly parthenogenetically; males are only known from the junior synonym *teretirostris* Stierlin, 1866 in the Seealps (mentioned by Stierlin in the description, but never revised since). The validity of several of the synonymous names is highly debated, part of them were recently resurrected in Magnano & Alonso-Zarazaga (2013). Such synonyms are *subdentatus* Bach, 1854 (described from Thuringia, Germany), *frigidus* Mulsant & Rey, 1859 (from the western Alps), *cyclopterus* F. Solari, 1946 (Tirol, Italy/Austria, Bayern, Germany) and the before mentioned *teretirostris*.

Describing every single population as a separate species cannot be the goal of studying biodiversity [in the cases of parthenogenetically reproducing populations (unfertilized eggs producing only females, and apomixis, where no meiosis is involved) we have mostly nearly identical genotypes (but see also last section of this part)]. We therefore included 15 samples of *O. pupillatus*, which resulted in four roughly separable genetic lineages, where three of them differ in few substitutions, and a single specimen from Grisons (sample 085) differs substantially from all others (K2 distances: 0.073-0.086). There is no morphological match with any of the before mentioned debatable species or morphotypes. The first clade comprises samples from the Central and Eastern Swiss Alps (samples 028, 054, 055, 065, 075, 084, 097, 124 from Valais, bordering Italy and Grisons), the second one a specimen from the Val Mustair (sample 106), the third specimens from the Bernese Alps and Lower Engadine (samples 007, 012, 042, 074, 088), and the fourth one (the most differing, as already mentioned), a single specimen from Central Grisons (sample 085). Well supported sister to all samples of *O. pupillatus* is *O. difficilis*, an amphigonic, also morphologically close standing species from northern Italy, Ticino up to the Valais in the Simplon region.

The same discrepancy between morphology and genetic lineages (the retrieved clades do not include specimens

sharing the same set of characters) was observed in *Otiorhynchus nodosus* (O. F. Müller, 1764) belonging to the subgenus *Postaremus* (K2 distances 0.068-0.07, Table 4). Not less than 12 synonymous names belong to this highly variable, boreo-alpine species (colour of legs from black to red, shape of body, vestiture). As already mentioned for *O. pupillatus*, *O. nodosus* is also parthenogenetic in most of its area, and throughout the Swiss Alps.

In both species mentioned, the observed well separated clades may more likely mirror several post glacial immigration lineages. An alternative explanation would be that these asexually reproducing species represent complexes of species in statu nascendi in the sense of Dobzhansky & Spassky (1959). A phenomenon reported just recently from an identically parthenogenetically reproducing entomine weevil: *Naupactus cervinus* Boheman, 1840 in South America (Rodríguez *et al.*, 2013). Thereby the presence of different evolutionary units correlating with faint morphological and ecological differences could be shown, driven by many well-known evolutionary forces as mutation, selection, drift going along with geographic isolation. Whatsoever, naming these purely genetically recognisable evolutionary units/populations will not (yet?) make sense, and unnecessarily blow up the taxonomy of *Otiorhynchus*. To gain a more complete insight into these complexes, definitely more samples from a broader geographical range and additional nuclear markers are needed.

Genus *Otiorhynchus* Germar, 1822 s. str.

All species samples from this subgenus clustered together, although with insufficient bootstrap support (Fig. 1, Supp. 1), including *O. morio* Fabricius, 1781, type species (!) of the subgenus *Phalantorrhynchus* Reitter, 1912, but morphologically hardly separable from *Otiorhynchus* s. str. This might show, as already suspected by the span of morphological differing members, and species only weakly differing from *Otiorhynchus* s. str. (as e.g. *O. tenebricosus* versus *O. putoni* Stierlin, 1891), that *Phalantorrhynchus* is a polyphyletic construct which needs to be thoroughly re-analysed in future.

In the case of the two samples of *Otiorhynchus* (s. str.) *meridionalis* Gyllenhal, 1834 included, one comes from Switzerland, Bern (sample 126), the other from southern France, Var (sample 129) and corresponds to the junior synonym *O. civis* Stierlin, 1861. This result uncovers a synonymy proposed by the first author in Pelletier (2005: 111) and later implemented in Magnano & Alonso-Zarazaga (2013). The type specimens of *O. civis* in the Gustav Stierlin collection (conserved in the Deutsches Entomologisches Institut, Müncheberg, Senckenberg) were examined in 2005, and one male specimen with the following label data “Gall. mer.” [*Gallia meridionale* = southern France] is selected, and is here designated as

lectotype, labelled with a red label: “LECTOTYPUS *Otiorhynchus civis* Stierlin 1861 des. C. Germann 2016”. The selection of the lectotype is of special importance, as Stierlin (1861) erroneously mentioned “Griechenland” [Greece] as type locality of *O. civis*. In his collection there was, among other specimens from southern France, also a female specimen from Greece determined as “*O. civis* Stl.”. However, *O. meridionalis* is not (yet probably, the species is currently spreading across Europe) known from Greece, and as already stated by Reitter (1913), the specimen from Greece is most likely mislabelled. Furthermore, it is a female specimen, whereas Stierlin (1861) clearly portrayed a male specimen in his description.

The examination of the penis, including the internal sac, did surprisingly not reveal any relevant differences in the two species (the main reason for the proposed synonymy in 2005), but the external morphology, supported here

by the molecular data, allows a differentiation between the two species. Therefore *Otiorhynchus civis* Stierlin, 1861 **stat. rev.** is removed from the synonymy with *O. meridionalis* Gyllenhal, 1834. Figure 3 shows both species, the broad elytra and the rugose surface and the denser grey hairs on elytra of *O. civis* (Fig. 3A) allows a differentiation from *O. meridionalis*, where the elytra are more elongate oval and shiny (Fig. 3B; a differentiation already given by Reitter, 1913: 44). *O. civis* is – after present knowledge and specimens examined – still restricted to southern France, whereas *O. meridionalis* is recorded more and more from surrounding countries (details in Magnano & Alonso-Zarazaga, 2013 under *meridionalis*).

The third species of the *O. meridionalis*-species group in our data set is *O. aurifer* Boheman, 1842, is also included in our dataset and it is well separated (Table 5).



Fig. 3. (A) *Otiorhynchus civis* Stierlin, 1861 stat. rev. (France, Var, Bargème). (B) *O. meridionalis* Gyllenhal, 1834 (Switzerland, Bern).

Tables 1-8: COI Kimura 2-Parameter genetic distances for a set of selected samples used in the present study. See the main text for further details.

Table 1: Apionidae

	<i>A. s.</i> 155	<i>A. s.</i> 141	<i>H. w.</i> 156	<i>H. w.</i> 146	<i>O. b.</i> 147
<i>Aizobius sedi</i> 155					
<i>Aizobius sedi</i> 141	0.027				
<i>Hemitrichapion waltoni</i> 156	0.182	0.189			
<i>Hemitrichapion waltoni</i> 146	0.180	0.188	0.011		
<i>Osellaus bonvouloirii</i> 147	0.170	0.174	0.196	0.192	
<i>Osellaus bonvouloiri bonvouloiri</i> 153	0.163	0.163	0.187	0.187	0.059

Table 2: selected *Dichotrachelus* samples

	<i>D. k.</i> 182	<i>D. k.</i> 081	<i>D. a.</i> 062	<i>D. a.</i> 089	<i>D. s.</i> 023	<i>D. m.</i> 093
<i>Dichotrachelus koziorowiczi</i> 182						
<i>Dichotrachelus koziorowiczi</i> 081	0.067					
<i>Dichotrachelus augusti</i> 062	0.151	0.163				
<i>Dichotrachelus augusti</i> 089	0.165	0.159	0.115			
<i>Dichotrachelus sondereggeri</i> 023	0.145	0.155	0.016	0.103		
<i>Dichotrachelus maculosus</i> 093	0.169	0.141	0.108	0.106	0.098	
<i>Dichotrachelus maculosus</i> 073	0.173	0.156	0.109	0.122	0.099	0.026

Table 3: *Hypera nigrirostris* species group

	<i>H. n.</i> 016	<i>H. o.</i> 098	<i>H. n.</i> 094	<i>H. m.</i> 091
<i>Hypera nigrirostris</i> 016				
<i>Hypera ononidis</i> 098	0.003			
<i>Hypera nigrirostris</i> 094	0.007	0.007		
<i>Hypera melarynchus</i> 091	0.010	0.010	0.012	
<i>Hypera nigrirostris</i> 019	0.012	0.009	0.010	0.013

Table 4: *Otiorhynchus nodosus*

	<i>O. n.</i> 027	<i>O. n.</i> 034	<i>O. n.</i> 041	<i>O. n.</i> 080	<i>O. n.</i> 107
<i>Otiorhynchus nodosus</i> 027					
<i>Otiorhynchus nodosus</i> 034	0.068				
<i>Otiorhynchus nodosus</i> 041	0.000	0.068			
<i>Otiorhynchus nodosus</i> 080	0.070	0.001	0.070		
<i>Otiorhynchus nodosus</i> 107	0.000	0.068	0.000	0.070	
<i>Otiorhynchus nodosus</i> 108	0.000	0.068	0.000	0.070	0.000

Table 5: *Otiorhynchus meridionalis* species group

	<i>O. aurifer</i> 170	<i>O. meridionalis</i> 126
<i>Otiorhynchus aurifer</i> 170		
<i>Otiorhynchus meridionalis</i> 126	0.142	
<i>Otiorhynchus civis</i> 129	0.132	0.093

Table 6: Sibling alpine species *Polydrusus paradoxus*/*Polydrusus chaerodrysius*

	<i>P. chaerodrysius</i> 143	<i>P. chaerodrysius</i> 103
<i>Polydrusus chaerodrysius</i> 143		
<i>Polydrusus chaerodrysius</i> 103	0.002	
<i>Polydrusus paradoxus</i> 032	0.048	0.048

Table 7: selected *Nebria* samples

	<i>N. f. rhaetica</i> 121	<i>N. c. escheri</i> 117	<i>N. heri</i> 114
<i>Nebria fontinalis rhaetica</i> 121			
<i>Nebria cordicollis escheri</i> 117	0.006		
<i>Nebria heeri</i> 114	0.011	0.018	
<i>Nebria cordicollis tenuissima</i> 123	0.010	0.016	0.002

Table 8: *Oreonebria breinii* vs *Oreonebria bluemplisalpicola*

	<i>O. bluemplisalpicola</i> 083	<i>O. bluemplisalpicola</i> 072	<i>O. breinii</i> 082
<i>Oreonebria bluemplisalpicola</i> 083			
<i>Oreonebria bluemplisalpicola</i> 072	0.015		
<i>Oreonebria breinii</i> 082	0.040	0.043	
<i>Oreonebria breinii</i> 071	0.040	0.043	0.000

Genus *Otiorhynchus* Germar, 1822
Subgenera *Nehrodistus* Reitter, 1912, *Misenatus* Reitter, 1912, *Melasemnus* Reitter, 1912

From subgenus *Nehrodistus* the four species *O. armatus* Boheman, 1842, *O. turca* Boheman, 1842, *O. obesus* Stierlin, 1861, and *O. pesarinii* Diotti, 2008 are included. These species did not form a monophyletic clade, and species of other subgenera e.g. *Otiolehus* cluster within (Fig. 1, Supp. 1). This may show that a natural group of relatives including species of *Nehrodistus* – mainly characterised by the toothed femora, the rugose pronotum, the spotty distributed scales on elytra, these deprived of hairs and the slender antennae with second article almost twice as long as first – may include species of other subgenera as well. However, the detailed relationships among these species are not supported by sufficient bootstrap values and remain therefore questionable with our COI sequence data.

In the case of *O. armatus* the sample from the Ligurian coast differed substantially (K2 distance: 0.077) from the one taken on Ischia island. Just recently Diotti (2008) revised the species close to *O. armatus* and described with *O. pesarinii* a new species from Basilicata. The subsequent comparison with a paratype specimen provided by the author, the con-specificity of the sample specimen from Ischia Island with *O. pesarinii* could be confirmed.

Interesting and surprising from the morphological point of view are *Otiorhynchus lugens* (Germar, 1817) and *O. ovalipennis* Boheman, 1842 as highly supported sister

taxa (ML and NJ both 99). Where a species with a single tooth on the femora, a slender rostrum, eyes laterally standing, elytra dull and deprived of hairs, and robust legs (subgenus *Misenatus*) is sister to *O. ovalipennis* (*Melasemnus*) with several additional small rasp like teeth on fore femora, a short rostrum, dorsally oriented eyes, shiny elytra with hairs, and gracile slender legs may represent unreliable characters for morphological estimates on phylogenetic relationships. The differences regarding teeth on femora is also present in the – although in both our analyses moderately supported – clade of *O. magnicollis* Stierlin, 1888 + *O. thaliarchus* Reitter, 1914 (*Choilisanus* Reitter, 1912 with unarmed femora, versus *Melasemnus* with teeth, often even several on fore femora). Another example for the absence and/or presence of teeth is the clade *Metopiorrhynchus* (teeth present) + *Aranihus* (teeth absent, or minute and often overlooked as in *O. ligneus*!) + pars *Phalantorrhynchus* (teeth absent) + *Nihus* (teeth absent), however with lower support (ML: 58; NJ: 61).

Genus *Polydrusus* Germar, 1817

We included five samples of this genus belonging to 3 species out of 2 subgenera (*Piezocnemus* Chevrolat, 1869 and *Chlorodrosus* K. Daniel & J. Daniel, 1898). The species were not retrieved in a monophyletic clade (Fig. 1, Supp. 1), suggesting that the species concept of *Polydrusus* is also polyphyletic, which is not really a surprise, regarding the span of morphological variability.

In the case of the sibling alpine species *Polydrusus paradoxus* Stierlin, 1859 / *chaerodrysius* Gredler, 1866 the differences in the COI support the very subtle morphological characters; both species can be distinguished mainly by the form of the scales on their femora (Germann, 2012). Thus it can be stated that small morphological differences are mirrored by a considerable genetic distance (K2 distance: 0.048). Furthermore, although from apparently very isolated populations, the samples of *P. chaerodrysius* collected in Valchava GR (sample 103) and Schwarenbach BE (208 km from each other; sample 143 / sample 063) differ in solely 0.2 % (Table 6). More localities were not discovered at present, despite of several specific excursions in-between. An explanation could be their parthenogenetical reproduction, where no gene-exchange as in sexual reproduction occurs.

species-pair *Phyllobius pyri* / *vespertinus*

The species status of *Phyllobius vespertinus* (Fabricius, 1792) was (and still is) highly debated (e.g. Dieckmann, 1979; Germann, 2011a; Alonso-Zarazaga, 2013) and recently regarded as synonym to *P. pyri* (Linné, 1758) (e.g. Colonnelli, 2003; Yunakov, 2013). While *Phyllobius pyri* lives mostly on arboreous Rosaceae and shows a more elongate body and a regularly coloured vestiture, *P. vespertinus* is more xerothermophilous, lives on various herbaceous plants, its body is more stout, the elytra often with a striped vestiture. We here included further specimens from the southern side of the Alps, where the characters of *P. vespertinus* are well pronounced [and from there (Monte Rosa, Val d'Entremont, St. Bernhard) once described as separate taxon *artemisiae* Desbrochers, 1873, junior synonym of *P. vespertinus*]. However, we provide further support that the taxa are not separable based on analyses of COI sequences (Fig. 1, Supp. 1), as already shown by Schütte *et al.* (2013). Similar to the *Hypera nigrirostris*-group, COI might be not sensitive enough to show differences, due to recent (ecological) separation of the taxa (i. e. incomplete lineage sorting), and/or genetical interchange (hybridisation) might still occur.

Family Carabidae Latreille, 1802

Subfamily Nebriinae Laporte, 1834

Genera *Nebria* Latreille, 1802,

Oreonebria K. Daniel, 1903

Both *Nebria* and *Oreonebria* are monophyletic and cluster together with good (ML) to strong (NJ) bootstrap support (Fig. 2, Supp. 2). In the case of the high-alpine *Nebria cordicollis* Chaudoir, 1837 -group, we here included three taxa: *N. heeri* K. Daniel, 1903, recently raised to species level from a subspecies of *cordicollis* by Szallies & Huber (2013), *N. cordicollis escheri* Heer,

1837 from southeastern Switzerland, and *N. cordicollis tenuissima* Bänninger, 1925, the westernmost populations in the Swiss Alps. All species of the *cordicollis*-group, as well as *N. fontinalis rhaetica* K. & J. Daniel, 1890 show conspicuously low interspecific K2 distances (0.002-0.018; Table 7).

As already mentioned by the authors (Szallies & Huber, 2014) in their very recent description of *O. buemlisalpicola*, the included samples are clearly separate (K2 distances: intraspecific = 0.0-0.015; interspecific: 0.04-0.043; Table 8) and belong to the eastern distributed *Oreonebria breinii*, whereas the western ones belong to *O. bluemlisalpicola*.

CONCLUSIONS

Coleoptera comprise about 35% of the total endemic animal species listed in Switzerland and more than 45% of all the listed Swiss endemic arthropod species (Germann *et al.*, 2013). The present project focused above all on relict populations of rare Alpine endemic (or potentially endemic) beetle species belonging particularly to the families Curculionidae and Carabidae (respectively 85% and 10% of all the samples included here).

The relationships within the species-rich family Curculionidae and within its large genus *Otiorhynchus* were overall not strongly supported in our analyses based on a relatively short fragment of the COI gene. However, the COI gene portion used here as DNA barcode was very useful to detect and discriminate single nominal species. Moreover, some further essential considerations could be done, especially focusing at the relationships within the identified monophyletic groups (which generally correspond to the proposed subgenera or species complexes). In several cases, incertitude at the morphological level was mirrored in the results recorded at the molecular genetic level as well. Outstanding examples are

- i) the parthenogenetical *Otiorhynchus pupillatus* lineages with probably several independent immigrations,
- ii) the *Hypera nigrirostris*-species group with *H. nigrirostris*, *H. ononidis* and *H. melarhynchus* merged,
- iii) the *Phyllobius pyri* / *vespertinus*-species complex.

Also in several cases species could be delimited or preliminarily approved as i) the alpine *Anthonomus rubi*-populations; *Otiorhynchus armatus* / *pesarinii*. Moreover, we found both, species with small morphological differences, associated with considerable genetic divergence (*Polydrusus paradoxus* / *chaerodrysius*), and morphologically accepted species (or subspecies) where only small differences were found in the investigated barcode sequences (*Nebria cordicollis* -group, *N. fontinalis*). In some cases, species considered as a single one, are in fact composed of two "cryptic species"

(*Otiorhynchus civis* / *O. meridionalis*, *Dichotrachelus koziorowiczi*, *D. angusti*).

We also provide support that in relatively immobile species and isolated populations definitely more diversity is detectable (*Osellaeus bonvouloirii*, *Dichotrachelus* spp.), an issue that should be addressed in future projects including further samples from restricted populations. Within several genera, where more species from partly different subgenera could be included (e.g. *Otiorhynchus*, *Dichotrachelus*, Hyperini), first preliminary insights of the systematics at genus/subgenus-level could be gained, together with insights on the phylogenetic value of certain morphological traits. In the traditional morphology, the presence or absence and the shape of teeth on femora in the genus *Otiorhynchus* is used as decisive character for discrimination of subgenera. Hence teeth (or no teeth) are used as traits providing a considerable phylogenetic signal. This is questionable after our results, and should be corroborated including nuclear markers and more key species from further subgenera.

Overall, thanks to this kind of DNA barcoding approach, it was definitely possible to reveal potential cryptic taxa and identify (genetically) isolated beetle populations. These results stimulate the re-thinking of relationships and enhance the formulation of new phylogenetic hypotheses, which should be corroborated, as usual, with morphological, ecological, and genetic data (with the promising inclusion of both mitochondrial and nuclear markers). For the near future, we plan to extend our data set with the addition of other key taxa, again with focus on the Alpine region.

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SUPPLEMENTARY DATA

Supp. 1. Neighbor-Joining tree (Kimura 2 parameter) based on COI sequences of 142 samples of Curculionoidea (Apionidae and Curculionidae) and Chrysomelidae obtained by using MEGA 6. Values (over 50%) of bootstrap support from 5 000 pseudo-replicates are depicted above nodes. Figure available trough <http://doi.org/10.5281/zenodo.153861>

Supp. 2 Neighbor-Joining tree (Kimura 2 parameter) based on COI sequences for 20 samples of Carabidae and Staphylinidae obtained by using MEGA 6. Values (over 50%) of bootstrap support from 10'000 pseudo-replicates are depicted above nodes. Figure available trough <http://doi.org/10.5281/zenodo.153861>

Annex 1. The 178 beetle samples belonging to the families Curculionidae (152 samples), Carabidae (18), Apionidae (6), Chrysomelidae (1), and Staphylinidae (1) sequenced in our study. Nr = NMLU-ENT000XXX. det. = determined by; Coordinates refer to the Swiss coordinates; leg. = collected by; Abbreviations: RC = Regula Cornu; CG = Christoph Germann; CH = Charles Huber; PS = Peter Sonderegger, AS = Alexander Szallies; MR = Miguel Richard; US = Ueli Schneppat. States are shortened following Löbl & Smetana (2013).

Nr.	Family/subfamily/species	det.	date			Locality	Coordinates		leg.	BOLD-nrs		
			d	m	y		N	E		COI		
Apionidae, Apioninae												
141	<i>Aizobius sedi</i>	CG	10	5	2013	FR, Ardèche, Les Ollières-sur-Eyrieux			CG		KU982998	
155	<i>Aizobius sedi</i>	CG	10	8	2010	SZ, Neuchâtel, Le Sordet	563286	206929	CG		KU982997	
146	<i>Hemitrichapion waltoni</i>	CG	19	4	2011	FR, Vacluse, Mt. Ventoux, NW Sault			CG		KU983045	
156	<i>Hemitrichapion waltoni</i>	CG	3	7	2010	IT, Piemonte, V. Formazza, V. di Morasco, Riale			CG		KU983044	
185	<i>Mesotrichapion punctirostre</i>	CG	8	7	2012	SZ, Valais, Termen, Fleischbode			CG		no data	
147	<i>Osellaeus b. bonvouloirii</i>	CG	14	6	2012	SZ, Isenthal, Brisen	677485	194549	CG		KU983075	
153	<i>Osellaeus b. bonvouloirii</i>	CG	1	4	2011	SZ, Plaffeien, Kaiseregg	590564	166604	CG		KU983076	
159	<i>Osellaeus b. bonvouloirii</i>	CG	5	8	2009	SZ, Zermatt, Gornegrat	93655	626327	CG		no data	
Carabidae, Nebriinae												
112	<i>Nebria picea</i>	AS	11	7	2012	SZ, Gridone			CH		KU983074	
117	<i>Nebria cordicollis escheri</i>	AS	8	8	2012	SZ, Alperschällilücke			AS		KU983062	
123	<i>Nebria cordicollis tenuissima</i>	CG	19	7	2012	SZ, Albristhorn			AS		KU983063	
121	<i>Nebria fontinalis rhaetica</i>	CG	14	8	2012	SZ, Rosenlauri-Gletscher			AS		KU983064	
114	<i>Nebria heeri</i>	AS	31	7	2012	SZ, Glärnisch			AS		KU983065	
118	<i>Oreonebria angustata</i>	AS	9	8	2012	SZ, Tambogletscher			AS		KU983066	
115	<i>Oreonebria angusticollis</i>	AS	18	7	2012	SZ, Cornettes de Bise			AS		KU983067	
72	<i>Oreonebria bluensisalpicola</i>	CG	16	7	2013	SZ, Grindelwald, below Wildgärist	648704	171141	AS		KU983069	
83	<i>Oreonebria bluensisalpicola</i>	CG		7	2013	SZ, Grindelwald, Schrybershömli			AS		KU983068	
71	<i>Oreonebria bremii</i>	CG	16	7	2013	SZ, Grindelwald, below Wildgärist	648704	171141	AS		KU983070	
82	<i>Oreonebria bremii</i>	CG		7	2013	SZ, Grindelwald, Schrybershömli			AS		KU983072	
113	<i>Oreonebria bremii</i>	AS	28	9	2006	SZ, Brienzler Rothorn			AS		KU983071	
120	<i>Oreonebria castanea raetzeri</i>	CG	5	7	2005	SZ, Jura, Les Verrières			AS		KU983073	
Carabidae, Pterostichinae												
122	<i>Pterostichus morio peirolerii</i>	CG	28	9	2006	SZ, Brienzler Rothorn			AS		KU983152	
116	<i>Pterostichus panzeri</i>	AS	8	7	2012	SZ, Silberen			AS		KU983153	
Carabidae, Trechinae												
134	<i>Trechus glacialis</i>	AS	26	5	2011	SZ, Tierwies			AS		no data	
137	<i>Trechus laevipes</i>	AS	23	10	2012	SZ, Baraghetto			AS		no data	

Nr.	Family/subfamily/species	det.	date			Locality	Coordinates		leg.	BOLD-nrs
			d	m	y		N	E		
133	<i>Trechus pertyi</i>	AS	14	8	2012	SZ, Rosenlaui-Gletscher			AS	KU983154
166	<i>Trechus piazzolii</i>	AS	11	7	2012	SZ, done			AS	KU983155
135	<i>Trechus schauini</i>	AS	9	8	2012	SZ, Tambogletscher			AS	KU983156
138	<i>Trechus schyberosiae</i>	AS	5	5	2011	SZ, Pilatus Oberhaupt			AS	no data
186	<i>Trechus tenuilimbatus</i>	AS	7	8	2012	SZ, Graubünden, Avers, Piotgletscher			AS	KU983157
Chrysomelidae, Chrysomelinae										
128	<i>Chrysolina lateincta vallesiaca</i>	CG	29	8	2013	SZ, Ulrichen, Nufenenpass, above Griessee, Mändeli	672090	146080	CG	KU983009
Cureulionidae, Ceutorhynchinae										
136	<i>Ceutorhynchus hutchinsiae</i>	CG	16	7	2013	SZ, Grindelwald, below Wildgärst	648704	171141	AS	KU983008
Curculionidae, Cryptorhynchinae										
14	<i>Echinodera samosa</i>	CG	1	4	2010	GR, Samos Isl., Oros Ambelos, Lazarou			CG	KU983043
Curculionidae, Curculioninae										
144	<i>Anthonomus rubi</i>	CG	10	7	2011	SZ, Amden, Mattstock	728655	225707	CG	KU983000
149	<i>Anthonomus rubi</i>	CG	25	6	2011	SZ, Kandersteg, Schwarenbach	615475	144084	CG	KU983003
150	<i>Anthonomus rubi</i>	CG	12	8	2011	SZ, Ftan, Piz Clüinas	814100	188854	CG	KU983001
152	<i>Anthonomus rubi</i>	CG	3	9	2011	SZ, Erlenbach, Stockhorn			CG	KU982999
157	<i>Anthonomus rubi</i>	CG	3	7	2010	IT, Piemonte, V. Formazza, V. di Morasco, Riale			CG	KU983002
181	<i>Anthonomus rubi</i>	CG	11	7	2009	SZ, BE, Stockhorn, Obere Walalp	606829	171711	CG	no data
151	<i>Tychius tridentinus</i>	CG	9	8	2011	SZ, Scuol, Foppas			CG	KU983158
Curculionidae, Cyclominae										
62	<i>Dichotrachelus augusti</i>	CG	8	9	2011	SZ, Orsières, Val Ferret, Ferret	576207	83488	CG	KU983012
69	<i>Dichotrachelus augusti</i>	CG	17	7	2012	SZ, Trient, Col de Balme, below Les Grandes Otaes			CG	KU983010
89	<i>Dichotrachelus augusti</i>	CG	15	10	2011	SZ, Saastal, Saas Fee, Galu	638580	105655	CG	KU983011
38	<i>Dichotrachelus imhoffi</i>	CG	16	9	2010	SZ, Pso. del Bernina, Giuf, below Piz Campase	799905	141715	CG	KU983013
81	<i>Dichotrachelus koziorowiczi</i>	CG	24	9	2011	FR, Corse, Zonza, Monte Calva			CG	KU983014
182	<i>Dichotrachelus koziorowiczi</i>	CG			2011	FR, Korsika, Col de Verghio			CG	KU983015
30	<i>Dichotrachelus lepointinus</i>	CG	4	7	2010	IT, V. Formazza, Vannino above Valdo, Cra della Dighetta	673154	137119	CG	KU983017
68	<i>Dichotrachelus lepointinus</i>	CG	14	9	2012	SZ, Berisal, S Bortelalp	650387	126518	CG	KU983016
36	<i>Dichotrachelus maculosus</i>	CG	1	4	2011	SZ, Plaffien, Kaiseregg	590564	166604	CG	KU983023
59	<i>Dichotrachelus maculosus</i>	CG	25	6	2011	SZ, Kandersteg, Schwarenbach	615475	144084	CG	KU983020
70	<i>Dichotrachelus maculosus</i>	CG	16	7	2013	SZ, Grindelwald, below Wildgärst	648704	171141	AS	KU983018
73	<i>Dichotrachelus maculosus</i>	CG	16	7	2013	SZ, Grindelwald, Schrybershömlli			CG	KU983019
92	<i>Dichotrachelus maculosus</i>	CG	5	5	2013	FR, Drôme, Vercors, Col de la Bataille			CG	KU983022

Nr.	Family/subfamily/species	det.	date			Locality	Coordinates			leg.	BOLD-nrs	
			d	m	y		N	E	COI			
93	<i>Dichotrachelus maculosus</i>	CG	5	5	2013	FR, Drôme, Vereors, Font d'Urle				CG	KU983021	
119	<i>Dichotrachelus maculosus</i>	CG	19	7	2012	SZ, Albristhorn				AS	KU983024	
26	<i>Dichotrachelus rudeni</i>	CG	5	8	2009	SZ, Zermatt, Gomergrat	93655	626327		CG	KU983026	
31	<i>Dichotrachelus rudeni</i>	CG	4	7	2010	IT, V. Formazza, Vannino above Valdo, Cra della Dighetta	673154	137119		CG	KU983027	
33	<i>Dichotrachelus rudeni</i>	CG	4	7	2010	IT, V. Formazza, Vannino above Valdo, W II Polmone	672940	136971		CG	KU983028	
47	<i>Dichotrachelus rudeni</i>	CG	15	7	2011	SZ, Trient, Col de Balme	564299	97168		CG	KU983029	
64	<i>Dichotrachelus rudeni</i>	CG	30	6	2012	SZ, Ilérémence, Col des Roux	595754	102045		CG	KU983030	
66	<i>Dichotrachelus rudeni</i>	CG	25	7	2012	SZ, Furkapass, Furfkastock, below	674959	158847		CG	KU983031	
67	<i>Dichotrachelus rudeni</i>	CG	8	9	2011	SZ, Orsières, Val Ferret, Ferret	576207	83488		CG	KU983025	
77	<i>Dichotrachelus rudeni</i>	CG	15	10	2011	SZ, Saastal, Saas Fee, Galu	638580	105655		CG	KU983033	
109	<i>Dichotrachelus rudeni</i>	CG	7	7	2013	SZ, NW-Disentis, Val da Lag Serein	705310	175720		CG	KU983032	
23	<i>Dichotrachelus sondereggeri</i>	CG	2	7	2009	SZ, Puschlav, ob. Cavaione, Corn dal Soleun	804489	126180		CG	KU983034	
25	<i>Dichotrachelus s.sulcipennis</i>	CG	5	8	2009	SZ, Zermatt, Gomergrat	93655	626327		CG	no data	
95	<i>Dichotrachelus variegatus</i>	CG		5	2013	IT, Lazio, Monti Lepini, Sempre-Visa				AS	KU983035	
139	<i>Dichotrachelus venturiensis</i>	CG	18	4	2011	FR, Vaucluse, Mt. Ventoux, below peak, E-exp. slope				CG	KU983036	
154	<i>Dichotrachelus venturiensis</i>	CG	18	4	2011	FR, Vaucluse, Mt. Ventoux, Chalet Reynard				CG	no data	
Curculionidae, Entiminae												
45	<i>Barynotus obscurus</i>	CG	23	7	2011	SZ, Brail, Prazet				CG	KU983004	
132	<i>Brachysomus samos</i>	CG	1	4	2010	GR, Samos Isl., Oros Ambelos, Lazarou				CG	KU983007	
21	<i>Otiorhynchus alpicola</i>	CG	4	6	2010	FR, Haut Jura, Gran Crêt	485675	126772		CG	no data	
90	<i>Otiorhynchus alpicola</i>	CG	6	8	2011	SZ, Tarasp, Avrona				CG	KU983077	
111	<i>Otiorhynchus alpicola</i>	CG	29	6	2013	SZ, Val Mora, below Piz dal Döss Radond	823323	162634		CG	KU983078	
51	<i>Otiorhynchus anthracinus</i>	CG	23	7	2011	SZ, Brail, Prazet				CG	KU983079	
40	<i>Otiorhynchus armadillo</i>	CG	6	8	2011	SZ, Tarasp, Avrona				CG	KU983082	
100	<i>Otiorhynchus armadillo</i>	CG	3	8	2013	SZ, Rubigen				CG	KU983080	
104	<i>Otiorhynchus armadillo</i>	CG	20	6	2009	SZ, Innertkirchen				CG	KU983081	
110	<i>Otiorhynchus armadillo</i>	CG	28	6	2013	SZ, Valchava, Val Vau, W-Praveder	824192	162000		CG	KU983083	
173	<i>Otiorhynchus armatus</i>	CG	25	9	2010	IT, Liguria, Savona, Finale Ligure, S. Bernardino				CG	KU983085	
174	<i>Otiorhynchus pesarinii</i>	CG				IT, Isola Isehia				US	KU983084	
170	<i>Otiorhynchus aurifer</i>	CG	17	9	2011	FR, Corse, Corte, Val Restonica, Camping de Tuani				CG	KU983086	
163	<i>Otiorhynchus caudatus</i>	CG				IT, Monteriggioni, Badesse				MR	KU983087	
2	<i>Otiorhynchus chrysocomus</i>	CG	20	6	2009	SZ, Gadmen				CG	no data	
145	<i>Otiorhynchus corsicus</i>	CG	18	9	2011	FR, Corse, Corte, Val Restonica, Lago Melu				CG	KU983088	

Nr.	Family/subfamily/species	det.	date			Locality	Coordinates			leg.	BOLD-nrs	
			d	m	y		N	E	COI			
171	<i>Otiorhynchus crataegi</i>	CG	20	6	2009	SZ, Innertkirchen				CG	KU983089	
8	<i>Otiorhynchus densatus</i>	CG	5	8	2009	SZ, Zermatt, Gornegrat	93655	626327		CG	no data	
35	<i>Otiorhynchus densatus</i>	CG	4	7	2010	IT, V. Formazza, Vannino above Valdo, above Il Polmone	672842	136328		CG	KU983090	
53	<i>Otiorhynchus desertus</i>	CG	12	8	2011	SZ, Ftan, Piz Clüinas	814100	188854		CG	KU983091	
148	<i>Otiorhynchus desertus</i>	CG	6	8	2011	SZ, Tarasp, Avrona				CG	no data	
125	<i>Otiorhynchus dieckmanni</i>	CG	3	9	2013	SZ, Bern, Naturhistorisches Museum, environments				CG	no data	
187	<i>Otiorhynchus difficilis</i>	CG		7	2011	SZ, Ticino, Lamone				CG	KU983092	
130	<i>Otiorhynchus ghiliani</i>	CG	22	4	2011	FR, Var, NW Fayence, Bargème, Montagnes de Brouis				CG	KU983093	
52	<i>Otiorhynchus gredleri</i>	CG	12	8	2011	SZ, Ftan, Piz Clüinas	814100	188854		CG	KU983095	
96	<i>Otiorhynchus gredleri</i>	CG	29	6	2013	SZ, Val Mora, below Piz dal Döss Radond	823323	162634		CG	KU983094	
50	<i>Otiorhynchus grischunensis</i>	CG	10	8	2011	SZ, Ftan, Piz Clüinas				CG	KU983096	
86	<i>Otiorhynchus intrusus</i>	CG	19	9	2011	FR, Corse, Porto, E Calanche, les roches bleues				CG	KU983097	
169	<i>Otiorhynchus juvenus</i>	CG	26	9	2011	FR, Corse, Ste. Lucie de P.V., Pinarellu				CG	no data	
48	<i>Otiorhynchus lepidopterus</i>	CG	23	7	2011	SZ, Brail, Prazet				CG	KU983098	
160	<i>Otiorhynchus ligustici</i>	CG				SZ, Churwalden				RC	KU983099	
161	<i>Otiorhynchus lugens</i>	CG				GR, Kerkyra				US	KU983100	
131	<i>Otiorhynchus magnicollis</i>	CG	1	4	2010	GR, Samos Isl., Oros Ambelos, Lazarou				CG	KU983101	
126	<i>Otiorhynchus meridionalis</i>	CG	3	9	2013	SZ, Bern, Naturhistorisches Museum, environments				CG	KU983103	
129	<i>Otiorhynchus civis</i>	CG	22	4	2011	FR, Var, NW Fayence, Bargème, Montagnes de Brouis				CG	KU983102	
9	<i>Otiorhynchus morio</i>	CG	11	7	2009	SZ, Stockhorn, Obere Walalp	606829	171711		CG	KU983104	
105	<i>Otiorhynchus mufi</i>	CG	28	6	2013	SZ, Val Mora, Döss Radond	823289	161728		CG	KU983105	
41	<i>Otiorhynchus nododus</i>	CG	6	8	2011	SZ, Tarasp, Avrona				CG	KU983106	
107	<i>Otiorhynchus nododus</i>	CG	28	6	2013	SZ, Valchava, Val Vau, W-Praveder	824192	162000		CG	KU983108	
108	<i>Otiorhynchus nododus</i>	CG	29	6	2013	SZ, Val Mora, below Piz dal Döss Radond	823323	162634		CG	KU983111	
27	<i>Otiorhynchus nododus</i>	CG	3	7	2010	IT, Piemonte, V. Formazza, Lago di Moraseo	673750	141390		CG	KU983109	
34	<i>Otiorhynchus nododus</i>	CG	4	7	2010	IT, V. Formazza, Vannino above Valdo, above Il Polmone	672963	136556		CG	KU983110	
80	<i>Otiorhynchus nododus</i>	CG			2011	SZ, Val Niemet, Ferrara				PS	KU983107	
127	<i>Otiorhynchus nubilus</i>	CG	29	8	2013	SZ, Ulrichen, Nufenenpass, above Griessee, Mändeli	672090	146080		CG	KU983112	
164	<i>Otiorhynchus obesus</i>	CG	6	4	2012	GR, Crete Island, Chania, Askifou-Plateau, Petres				CG	KU983113	
172	<i>Otiorhynchus ovalipennis</i>	CG	31	3	2010	GR, Athen, Airport, environments				CG	KU983114	
178	<i>Otiorhynchus ovatus</i>	CG	16	11	2012	SZ, Mörel, Salzgäb				CG	KU983115	
177	<i>Otiorhynchus pinastri</i>	CG	26	6	2010	SZ, Thun, Aareufer				CG	no data	
162	<i>Otiorhynchus porcatus</i>	CG				SZ, Churwalden				RC	no data	

Nr.	Family/subfamily/species	det.	date			Locality	Coordinates			leg.	BOLD-nrs	
			d	m	y		N	E	COI			
1	<i>Otiorhynchus pupillatus</i>	CG	20	6	2009	SZ, Gadmen				CG		no data
6	<i>Otiorhynchus pupillatus</i>	CG	6	8	2009	SZ, Habkern, Grünenbergpass	631996	178264		CG		no data
7	<i>Otiorhynchus pupillatus</i>	CG	28	6	2009	SZ, Sigriswil, Sigriswilergrat, Alpiglen				CG		KU983130
11	<i>Otiorhynchus pupillatus</i>	CG	-	8	2009	SZ, Reutigen, Lengenberg	611546	171965		CG		no data
12	<i>Otiorhynchus pupillatus</i>	CG	23	8	2009	SZ, Grindelwald, Brandegg	643715	162095		CG		KU983129
28	<i>Otiorhynchus pupillatus</i>	CG	3	7	2010	IT, Piemonte, V. Formazza, Lago di Morasco	673750	141390		CG		KU983127
42	<i>Otiorhynchus pupillatus</i>	CG	6	8	2011	SZ, Tarasp, Avrona				CG		KU983124
54	<i>Otiorhynchus pupillatus</i>	CG	12	8	2011	SZ, Ftan, Piz Clüinas	814100	188854		CG		KU983120
55	<i>Otiorhynchus pupillatus</i>	CG	23	7	2011	SZ, Brail, Prazet				CG		KU983119
65	<i>Otiorhynchus pupillatus</i>	CG	25	7	2012	SZ, Furkapass, Furkastock, below	674959	158847		CG		KU983116
74	<i>Otiorhynchus pupillatus</i>	CG	16	7	2013	SZ, Grindelwald, Schrybershörmli				CG		KU983117
75	<i>Otiorhynchus pupillatus</i>	CG	12	7	2012	SZ, Kandersteg, Sehwarenbach				CG		KU983118
84	<i>Otiorhynchus pupillatus</i>	CG	17	7	2012	SZ, Trient, Col de Balme, towards Tête de Balme				CG		KU983121
85	<i>Otiorhynchus pupillatus</i>	CG	15	8	2012	SZ, Riom, in garden				RC		KU983122
88	<i>Otiorhynchus pupillatus</i>	CG	19	6	2011	SZ, Kandersteg, Gasterental				CG		KU983123
97	<i>Otiorhynchus pupillatus</i>	CG	7	7	2013	SZ, NW-Disentis, Val da Lag Serein				CG		KU983126
106	<i>Otiorhynchus pupillatus</i>	CG	28	6	2013	SZ, Valehava, Val Vau, W-Praveder	824192	162000		CG		KU983128
124	<i>Otiorhynchus pupillatus</i>	CG	29	8	2013	SZ, Ulriehen, Zum Loeh				CG		KU983125
168	<i>Otiorhynchus pupillatus</i>	CG		9	2013	SZ, Noiraigue vers Creux du Van				CG		no data
176	<i>Otiorhynchus salicicola</i>	CG				SZ, Churwalden				RC		KU983131
175	<i>Otiorhynchus scaber</i>	CG	6	8	2009	SZ, Habkern, Grünenbergpass				CG		no data
102	<i>Otiorhynchus singularis</i>	CG	1	8	2013	SZ, Gstaad, Hintereggli, Mühlesteini				CG		KU983132
4	<i>Otiorhynchus subcostatus</i>	CG	2	7	2009	SZ, Puschlav, above Cavaione, Corn dal Soleun	804489	126180		CG		no data
18	<i>Otiorhynchus subcostatus</i>	CG	4	6	2010	FR, Haut Jura, Montoisey	486364	127500		CG		no data
3	<i>Otiorhynchus tenebricosus</i>	CG	20	6	2009	SZ, Gadmen				CG		no data
10	<i>Otiorhynchus tenebricosus</i>	CG	11	7	2009	SZ, Stockhorn, Obere Walalp	606829	171711		CG		KU983135
58	<i>Otiorhynchus tenebricosus</i>	CG	19	6	2011	SZ, Kandersteg, Gasterental				CG		KU983133
76	<i>Otiorhynchus tenebricosus</i>	CG	12	7	2012	SZ, Kandersteg, Sehwarenbach				CG		KU983134
78	<i>Otiorhynchus tenebricosus</i>	CG	14	6	2012	SZ, Isenthal, Brisen	677485	194549		CG		KU983136
165	<i>Otiorhynchus thaliarchus</i>	CG	6	4	2012	GR, Crete Island, Chania, Askifou-Plateau, Petres				CG		KU983137
60	<i>Otiorhynchus tirolensis</i>	CG	6	8	2011	SZ, Tarasp, Avrona				CG		KU983138
167	<i>Otiorhynchus turca</i>	CG				BG, Sofia Plain, City area, Knyazhevo				US		KU983139
158	<i>Otiorhynchus uncinatus</i>	CG	4	6	2010	FR, Haut Jura, Gran Crêt	485675	126772		CG		no data

Nr.	Family/subfamily/species	det.	date			Locality	Coordinates			leg.	BOLD-nrs	
			d	m	y		N	E	COI			
5	<i>Otiorhynchus varius</i>	CG	2	7	2009	SZ, Puschlav, above Cavaione, Corn dal Soleun	804489	126180	CG		KU983140	
15	<i>Phyllobius pyri</i>	CG	12	5	2010	SZ, Satigny, Montfleury	493701	119317	CG		KU983141	
179	<i>Phyllobius pyri</i>	CG				SZ, Churwalden			US		KU983142	
180	<i>Phyllobius pyri</i>	CG				SZ, Chur, Kalkofen			US		KU983143	
13	<i>Phyllobius vespertinus</i>	CG	22	5	2010	SZ, Val Blenio, Dongio	716000	144000	CG		KU983145	
39	<i>Phyllobius vespertinus</i>	CG	24	4	2011	IT, Valle d'Aosta, ob. Aosta			CG		KU983146	
61	<i>Phyllobius vespertinus</i>	CG	21	4	2011	FR, Var, E Le Muy, Bois de Malvoisin, Gorges du Blavet			CG		KU983144	
44	<i>Polydrusus amoenus</i>	CG	23	7	2011	SZ, Prazet			CG		KU983147	
63	<i>Polydrusus chaerodrysius</i>	CG	12	7	2012	SZ, Kandersteg, Schwarenbach			CG		KU983149	
103	<i>Polydrusus chaerodrysius</i>	CG	28	6	2013	SZ, Valehava, Val Vau, W-Praveder	824192	162000	CG		KU983148	
143	<i>Polydrusus chaerodrysius</i>	CG	25	6	2011	SZ, Kandersteg, Schwarenbach	615475	144084	CG		KU983150	
32	<i>Polydrusus paradoxus</i>	CG	3	7	2010	IT, V. Formazza, V. di Morasco, Riale	674420	142160	CG		KU983151	
Curculionidae, Hyperinae												
22	<i>Brachypera vidua</i>	CG	24	4	2010	SZ, Biel, Pavillon	584070	220480	CG		KU983005	
56	<i>Brachypera vidua</i>	CG	21	4	2011	FR, Var, E Le Muy, Bois de Malvoisin, Gorges du Blavet			CG		KU983006	
183	<i>Donu cyrtus</i>	CG	5	4	2010	GR, Samos Isl., Oros Kerkis, E-Vigla			CG		KU983037	
37	<i>Donus globosus</i>	CG	26	9	2010	IT, Liguria, Savona, Finale Ligure, C. di Melogno, Brieco della Guardia			CG		KU983039	
46	<i>Donus globosus</i>	CG	16	4	2011	FR, Vaueluse, Bedoin, Crillon-le-Brave			CG		KU983038	
49	<i>Donus globosus</i>	CG	17	4	2011	FR, Vaueluse, Gorges de la Nesque, Monieux			CG		KU983040	
20	<i>Donus ovalis</i>	CG	4	6	2010	FR, Haut Jura, Gran Crêt	485675	126772	CG		KU983041	
99	<i>Donus segnis</i>	CG	28	6	2013	SZ, Valehava, Val Vau, Spi da Vau	826000	164000	CG		KU983042	
29	<i>Hypera arator</i>	CG	27	6	2010	SZ, Neuchâtel, L'Ermitage	561800	205700	CG		KU983046	
140	<i>Hypera diversipunctata</i>	CG	5	5	2013	FR, Drôme, Vercors, Col de la Bataille			CG		KU983047	
142	<i>Hypera gracilentata</i>	CG	8	4	2013	PT, Loulé, Pena, Rocha da Pena			CG		KU983048	
79	<i>Hypera melancholica</i>	CG	21	4	2011	FR, Var, E Le Muy, Bois de Malvoisin, Gorges du Blavet			CG		KU983049	
91	<i>Hypera melarynchus</i>	CG	12	4	2013	PT, W Sagres, Cabo S. Vicente, resthouse			CG		KU983050	
43	<i>Hypera miles</i>	CG	23	7	2011	SZ, Brail, Prazet			CG		KU983051	
16	<i>Hypera nigrirostris</i>	CG	12	5	2010	SZ, Satigny, Montfleury	493701	119317	CG		KU983054	
19	<i>Hypera nigrirostris</i>	CG	4	6	2010	FR, Haut Jura, Gran Crêt	485675	126772	CG		KU983052	
94	<i>Hypera nigrirostris</i>	CG	13	4	2013	PT, W Lagos, Budens Umgb			CG		KU983053	
98	<i>Hypera ononidis</i>	CG	1	8	2013	SZ, Gstaad, Hintereggli, Mühlesteini			CG		KU983055	
57	<i>Hypera plantaginis</i>	CG	10	7	2011	SZ, Amden, Mattstock	728655	225707	CG		KU983056	

Nr.	Family/subfamily/species	det.	date			Locality	Coordinates		leg.	BOLD-nrs
			d	m	y		N	E		
87	<i>Hypera plantaginis</i>	CG	16	11	2012	SZ, Mörel, Salzgäb			CG	KU983057
17	<i>Hypera striata</i>	CG	12	5	2010	SZ, Vallon de l'Allondon, Malval, Les Granges	488856	119489	CG	KU983058
24	<i>Hypera venusta</i>	CG	4	6	2010	FR, Haut Jura, Montoisey	486364	127500	CG	KU983059
101	<i>Hypera venusta</i>	CG	29	6	2013	SZ, Val Mora, below Piz dal Döss Radond	823323	162634	CG	KU983060
Staphylinidae, Aleocharinae										
184	<i>Leptusa pilatensis</i>	AS	3	5	2006	SZ, Neuchâtel, Villiers			AS	KU983061

A new species of the genus *Typhlocharis* Dieck, 1869 (Coleoptera, Carabidae) from Portugal

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Abstract: A new endogean carabid species of the genus *Typhlocharis* Dieck, 1869 from Portugal is described and illustrated: *Typhlocharis mendesi* sp. n. The work provides diagnostic characters, the structure of male and female genitalia, discussions on affinities to related taxa, as well as some remarks on its ecology.

Keywords: Taxonomy - species Groups - Iberian Peninsula - Portugal.

INTRODUCTION

Within the Anillini, the genus *Typhlocharis* Dieck, 1869 (Coleoptera: Carabidae: Trechinae) is the most speciose in the Iberian Peninsula, with 63 known species (Serrano & Aguiar, 2014; Zaballos *et al.*, 2016). Ortuño & Gilgado (2011) provided a historical review of the genus. A synthesis on the current knowledge (e.g. updated descriptions, systematics reorganization, antennal morphology and chaetotaxy) and a review of the presence/absence of the last abdominal sternum ‘belt’, including remarks on its external microsculpture was provided by Serrano & Aguiar (2014). The aim of this work is to describe a new species of the genus *Typhlocharis* from Portugal and to discuss its taxonomic position within the traditional species groups.

MATERIAL AND METHODS

Fieldwork was conducted in Bucelas region located in the outskirts of Lisbon (Province of Ribatejo), resulting in the collection of specimens of an endogean beetle species of the subtribe Anillina. The specimens were collected by hand under embedded stones. Additional specimens were obtained from samples of soil taken under the embedded stones using Berlese apparatus. After careful study, we concluded that the specimens represent a new species of the genus *Typhlocharis*. Habitat description (soil and vegetation) can be accessed in Serrano & Aguiar (2012). The morphological study of dried and gold coated adult

specimens was conducted using a scanning electron microscope (SEM) JEOLJSM-5200 LV (JEOL Ltd Tokyo, Japan). The chaetotaxy of labrum, clypeus, anterior and posterior margins of pronotum, and posterior margin of last ventrite, follows the nomenclature proposed by Pérez-González & Zaballos (2012). However, we do not follow this nomenclature for the anterior margin of the prosternum due to its constancy and lack of relevance in terms of sexual dimorphism. Nomenclature of antennal features follows Pérez-González & Zaballos (2013a). Measurements were done with a Wild M5 stereoscopic microscope equipped with a dissecting microscope ocular micrometre. The male genitalia was mounted on 100% glycerol, and imaged on a Leica SPE confocal microscope, using a 40x 1.15NA oil-immersion objective. Optical slices were acquired every 0.5 µm. The z-stack was processed and 3D reconstructed using the Amira v5.3 software. The last female ventrite, the spermatheca, and the spermathecal gland were mounted on 100% glycerol and examined with a Zeiss Stereo Lumar V12 stereomicroscope. Coordinates of localities where specimens were found are indicated in U.T.M. (1 km x 1 km). Material examined is deposited in the collections with acronyms listed below:
cAS Coll. Artur Serrano, Faculty of Sciences, Lisboa, Portugal
MHNG Muséum d’histoire naturelle, Genève, Switzerland

TAXONOMY

Typhlocharis mendesi sp. n.

Figs 1-17

Holotype: cAS; 1 ♂; Portugal, Bucelas (Estremadura Prov.) (UTM: 29SMD9305), 3.III.2011, Serrano & Aguiar leg.

Paratypes: cAS; 3 ♂♂ and 2 ♀♀; same locality and date as holotype. – MHNG; 2 ♂♂ and 2 ♀♀; same locality and date as holotype. – cAS; 4 ♂♂ and 2 ♀♀; Bucelas (Estremadura Prov.) (UTM: 29SMD9305), 22.III.2011. – cAS; 3 ♂♂ and 4 ♀♀; Arruda dos Vinhos (Estremadura Prov.) (UTM: 29SMD9012), 3.III.2011. – cAS; 1 ♂; A. do Mourão (Estremadura Prov.) (UTM: 29SMD9209), 3.III.2011. – cAS; 1 ♀; Bucelas (Estremadura Prov.) (UTM: 29SMD9205), 23.X.2012. – cAS; 5 ♂♂ and 5 ♀♀ (2 ♂♂ and 2 ♀♀ gold coated); Bucelas (Estremadura Prov.) (UTM: 29SMD9305), 7.XII.2012. – MHNG; 1 ♂ and 1 ♀; same locality and date as previous lot. – cAS; 7 ♂♂; 7 ♀♀; Bucelas (Estremadura Prov.) (UTM: 29SMD9305). 1.XI.2013. All Serrano & Aguiar leg.

Diagnosis: Anophthalmous. Body parallel, depressed, brown or brownish-yellow with integument micro-reticulate and scattered pubescence. Antennae moniliforme. Semilunar notch present. Vertex with *pars stridens*. Pronotum rectangular (1.2 times longer than wide). Apical edge of elytra slightly sinuate, without teeth; discal setae arranged in 4 or 5 rows slightly bent anteriorly; umbilicate series with six (4+2) marginal setae; abdominal female sternum II and III with lateral fovea; anterior region of the last abdominal sternum in both sexes showing a smooth or scaly and serrate microsculpture ('belt') (Figs 13, 14). Hind trochanters inerm in both sexes (Figs 7-8). Aedeagus (Figs 15, 16) sickle-shaped, basal lamina markedly arcuate, the apex slightly eagle's beak shaped (lateral view); parameres bisetulose. Female genitalia (Fig. 12) with long tubular gonocoxites, each one with a double apical seta and without a lateral seta.

Etymology: This new species is dedicated to our colleague Luís Mendes, eminent Portuguese entomologist, who has been greatly contributing to the taxonomic and faunistic knowledge of the world Zygentoma, Microcoryphia, and Afrotropical Lepidoptera.

Description:

Length of holotype: 1.14 mm.

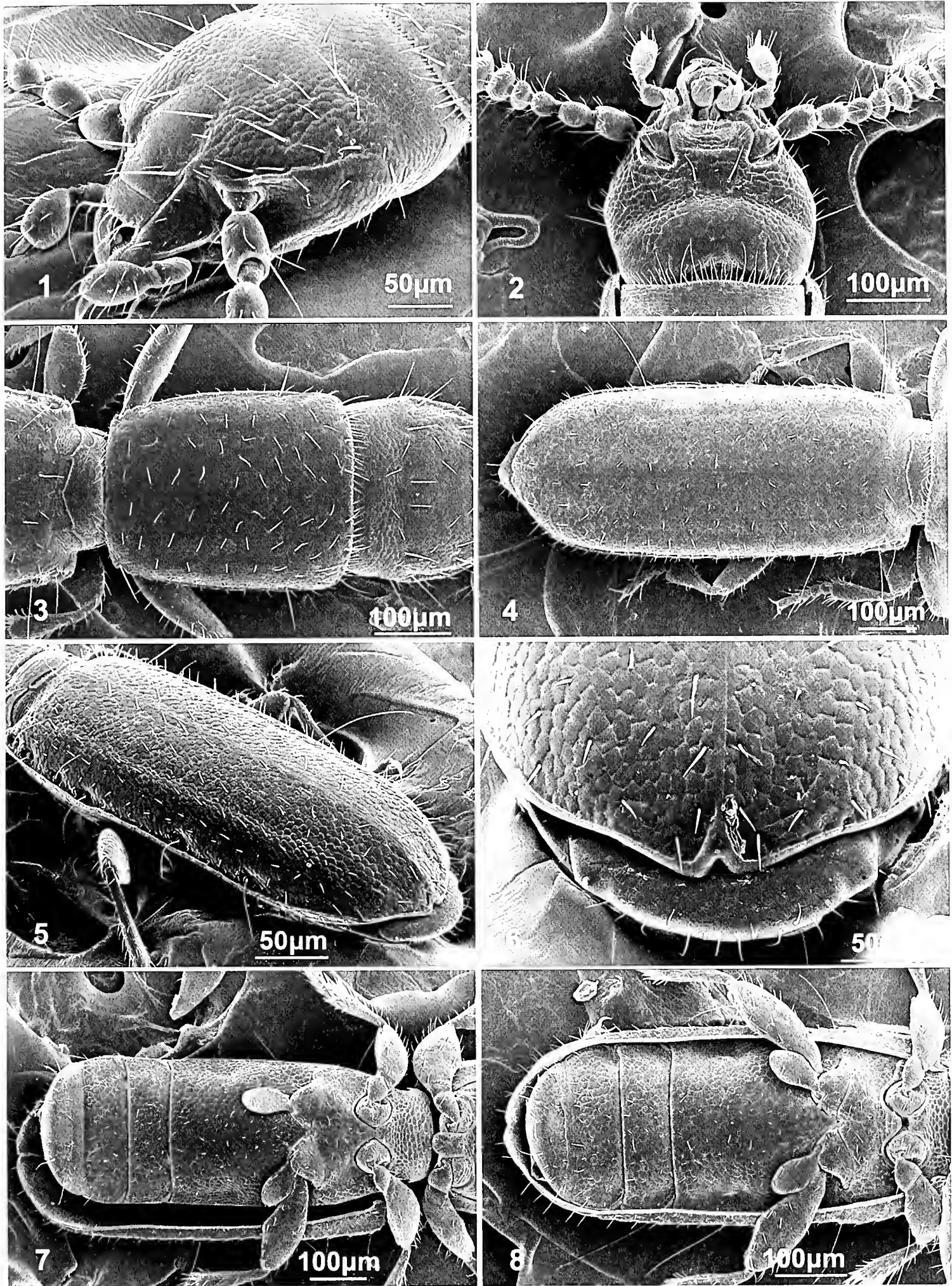
Length of paratypes: 1.12-1.23 mm (males) and 1.15-1.27 mm (females).

Head (Figs 1, 2, 9, 10): Almost as long as wide [length: 0.21-0.24 mm (males) and 0.22-0.26 mm (females), width: 0.24-0.26 mm (males) and 0.24-0.27 mm (females)] with hexagonal microsculpture; vertex with transverse microsculpture which, in the middle area below the anterior margin of the pronotum, is arranged

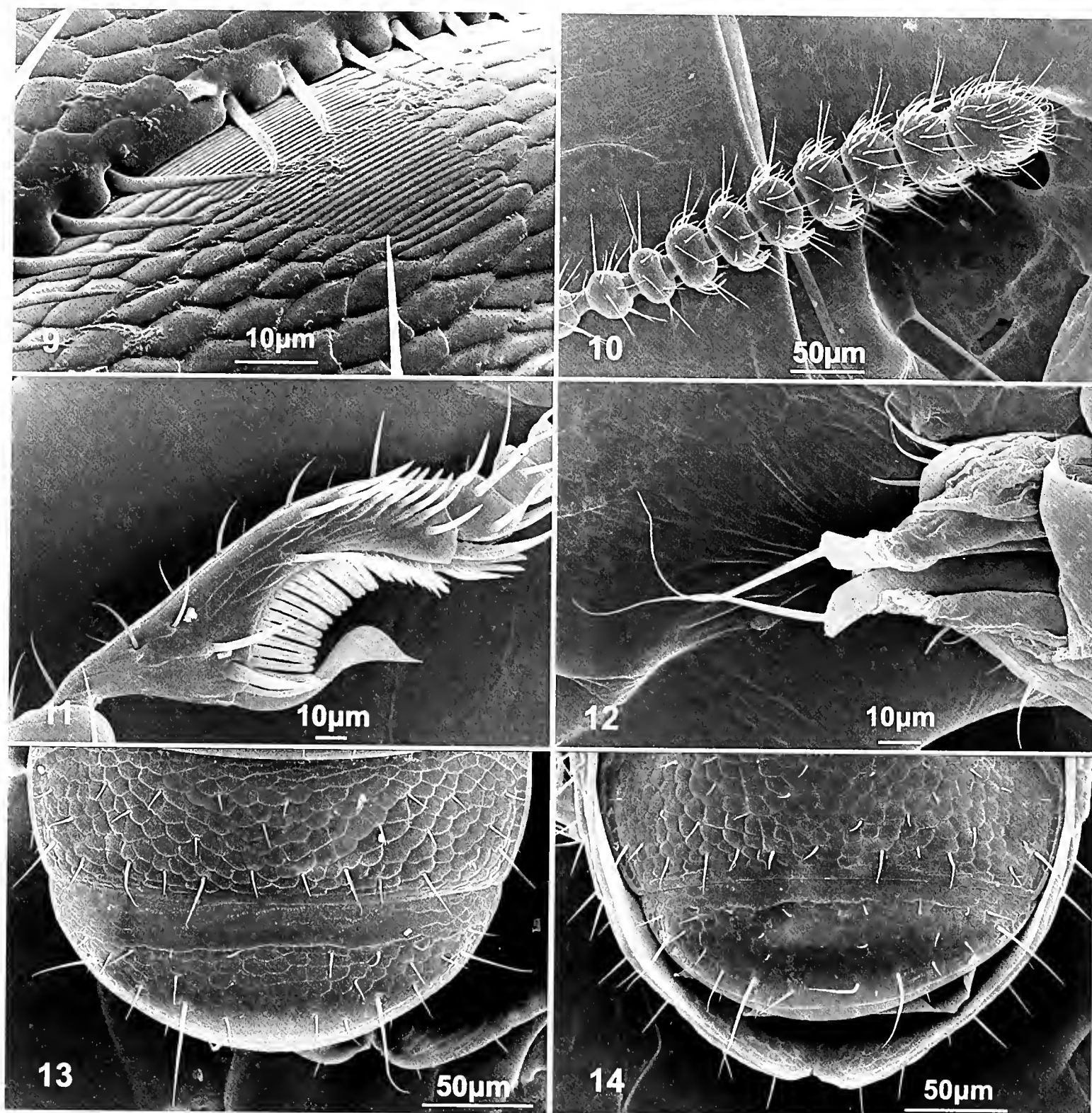
in parallel ridges forming a stridulatory organ (*pars stridens*) (Fig. 9); posterolateral region of the head with a semilunar notch (Fig. 1); labrum sub-rectangular, anterior margin almost straight; anterior margin of clypeus almost straight; moniliform antennae with 11 rounded antennomeres progressively more quadrate (morph 1, subquadrate, as defined in Pérez-González & Zaballos, 2013a), except last one, pyriform (Fig. 10). The last antennomere has a pattern of three anterodorsal and one posterodorsal sensilla coeloconica (type A). Ventral sensilla coeloconica in antennomeres 5° and 6°. Stem of third antennomere short (average proportion of stem length/antennomere body length=0.38). Labium with epilobes and middle tooth slightly sharp. Ligula with convex middle lobe and paraglossae not long. Gula wide with sutures visible through light microscopy. Cephalic chaetotaxy: two pairs of submarginal labral setae (l-s/s-l) and two pairs of marginal labral setae (m-m/m-m), two pairs of clypeal setae (l-s/s-l), one pair close to frontal sulcus; two pairs of supraocular setae (anterior and posterior) and 1-2 pairs of setae on the posterior region between vertex and lateral carinae.

Pronotum (Fig. 3): Rectangular, slightly longer than wide [length: 0.3-0.33 mm (males) and 0.31-0.34 mm (females); width: 0.26-0.28 mm (males) and 0.27-0.29 mm (females)], with hexagonal microsculpture, lateral margins slightly arcuate, slightly narrowed posteriorly, with 3-4 small crenulations before the posterior angles, which are marked with one small tooth; disk flattened, anterior margin almost straight and posterior margin slightly arcuate outwards in median region, anterior margin with medial hiatus. Pronotal chaetotaxy: four longitudinal series of erect setae between midline and lateral margins, directed inwards and slightly anteriorly; lateral groove of each side with one long seta in the anterior quarter and one long seta on hind angle; a row of five pairs of setae (l-l-l-l-l-l-l-l) parallel to the anterior margin, two pairs of setae near the posterior margin (l-l/l-l); a row of regularly placed setae in anterior, posterior and lateral margins, more spaced in the later.

Elytra (Figs 4, 5, 6): 2.1 times longer than wide [length: 0.58-0.65 mm (males) and 0.59-0.66 mm (females); width: 0.22-0.30 mm (males) and 0.29-0.30 mm (females)], parallel and oval posteriorly, dorso-ventrally flattened on the disk; transverse scutellar organ present; disk with hexagonal and pentagonal micro-sculpture, almost scaly in the lateral regions; scutellar region not punctured; humeral angles rounded; lateral margins serrate, the teeth decreasing in size posteriorly; apical margin without teeth. Elytral chaetotaxy: Part of the pubescence of the disk is arranged since the sutural region in four or five rows of short setae slightly directed anteriorly; a very irregular series of minute setae between the outer row and the lateral margins directed outward; umbilicated series aggregated with four seta in the anterior group and two in the posterior group (4+2) (Figs 4, 5).



Figs 1-8. *Typhlocharis mendesi* sp. nov. (1) Head in dorso-lateral view. (2) Head in ventral view. (3) Pronotum in dorsal view. (4) Elytra in dorsal view. (5) Elytra in dorso-lateral view. (6) Elytra in apical view. (7) Male abdomen in ventral view. (8) Female abdomen in ventral view.



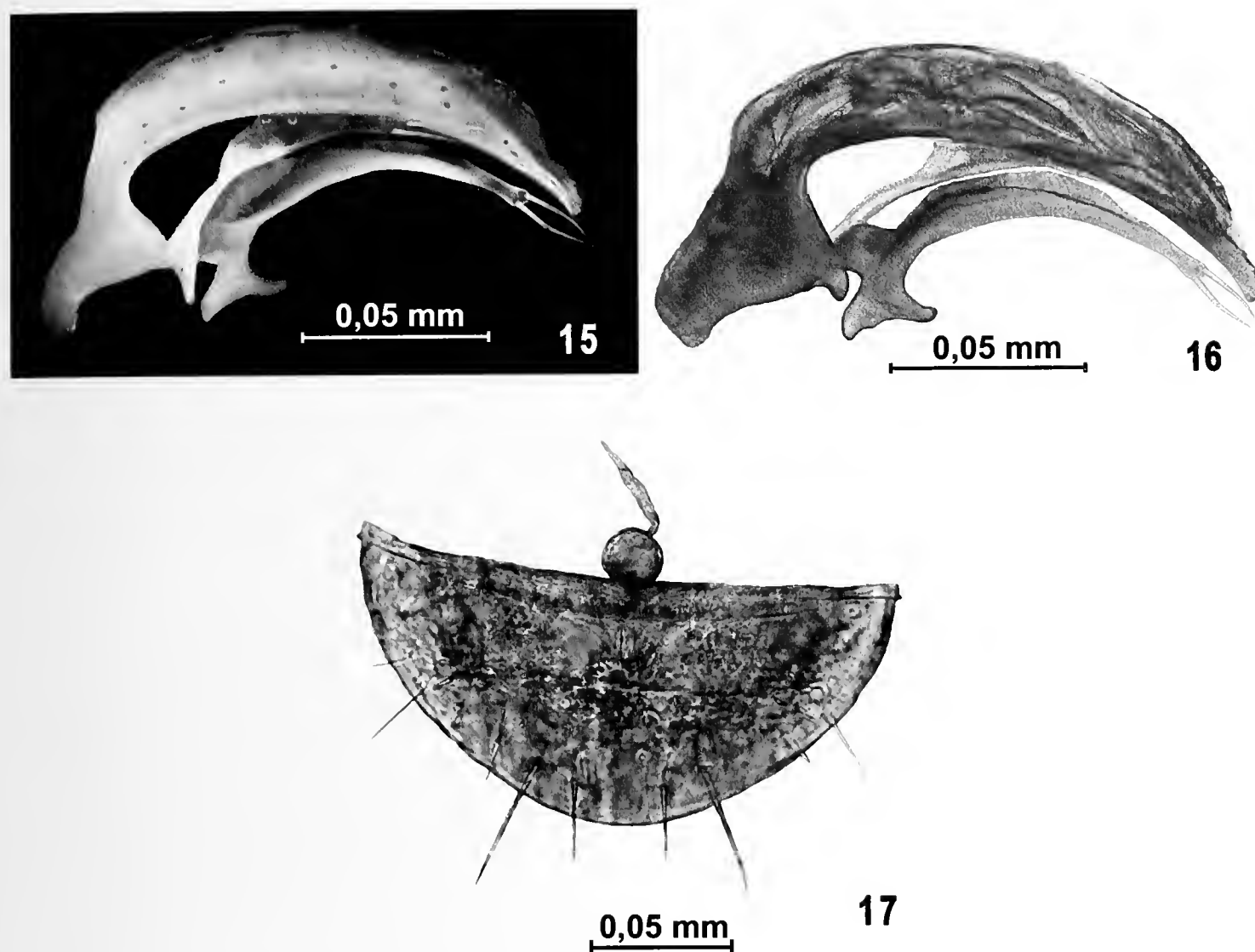
Figs 9-14. *Typhlocharis mendesi* sp. nov. (9) Stridulatory organ (*pars stridens*) in dorso-lateral view. (10) Antenna in dorsal view. (11) Male protibia cleaning organ in ventral view. (12) Female genitalia gonocoxites with apical setae in ventral view. (13) Male abdominal 'belt' in ventral view. (14) Female abdominal 'belt' in ventral view.

Legs: Femora robust, inner margin of pro- and meso-femora inerm, slightly dentate in metafemora; metatrochanters similar in both sexes and without any special features (Figs 7, 8); meso- and metatibiac without apical teeth (Figs 7, 8); apex of fore tibia with a comb of setae (cleaning organ) similar in both sexes (Fig. 11); male protarsus without dilated segments.

Abdomen (Figs 7, 8): Sterna II and III with lateral fovea, deeper in females than in males; last abdominal sternite (both sexes) presents in its anterior region a more or less

invaginated area of smooth and scaly zone of microtrichia (abdominal 'belt') (Figs 13, 14); last sternite chaetotaxy with sexual dimorphism: male (s-l-s-s-l(s)s/s(s)-l-s-s-l-s), female (s-l-s-s-l(m)m/m-l-s-s-l-s) (Figs 13, 14).

Male genitalia (Figs 15, 16): in lateral aspect with median lobe sickle-shaped, basal lamina markedly arcuate, the apex slightly shaped like an eagle's beak; in dorsal aspect with apex broadly rounded, slightly bent to left; internal sac with several tangled membranes, in central area with one twisted sclerite in continuous by



Figs 15-17. *Typhlocharis mendesi* sp. nov. (15) Aedeagus in external and lateral view. (16) Internal sac of median lobe in lateral view. (17) Spermatheca, spermathecal gland and last ventrite in ventral view.

one fusiform membrane (Fig. 16); parameres bisetulose apically; external tegument of median lobe with several presumably chemo- or chemo-mechano sensilla sunken in pits (Fig. 15). Ring sclerite (IX abdominal sternum) subtriangular-arcuate, the apical margin is slightly projected in a triangular blunt extension, gently tilted.

Female genitalia (Fig. 12): Tubular ovipositor gonocoxites weakly sclerotized, each one in ventral aspect without a lateral seta and with a double apical one (Fig. 12); internal genital tract with spermathecal duct short, spermatheca spherical (Fig. 17) and short (length: 0.022 mm); conical spermathecal gland (length: 0.047 mm) sclerotized in distal region (Fig. 17).

Variability: There is a certain degree of intraspecific variation affecting some characters, such as the chaetotaxy of the labrum, the number and marking of posterolateral denticles in the pronotum (from faintly marked to almost absent), or the chaetotaxy of the last ventrite, showing some variability of the number and length of marginal seta. It is also common that some

individuals show short and long setae irregularly mixed in the anterior row of setae in pronotum.

DISCUSSION

The following traits and others more have been used to discuss affinities among *Typhlocharis* species or to justify their close geographical proximity or even syntopy (Ortuño & Gilgado, 2011; see also Andújar *et al.*, 2010): conformation of clypeus, presence or absence of *pars stridens*, type of gula, discal setae on the elytron, elytral pores, tarsal formula, hind trochanter shape, sexual dimorphism [e.g. presence or not of: 1) a median tubercle or carina in the sternum II (males), 2) a more or less deep foveae in the sterna II, III or even IV (predominantly in females) and, 3) thorn-shaped hind trochanter (males); different chaetotaxy of the last abdominal segment].

Being useful for practical purposes, the morphological species groups proposed by Zaballos & Ruíz-Tapiador (1997), Zaballos & Wrase (1998), and more recently

by Pérez-González & Zaballos (2013b), are not always coherent, sometimes even for the geographic distribution of the species within each group (e.g. Zaballos & Pérez-González, 2011). This is evident, for instance, for the *diecki*- and *outereloi*-groups, whose diagnoses are based almost exclusively on the presence of a maximum number of two teeth in the apical margin of each elytron and on the pattern of the umbilicate series (4+3 – *diecki*-group, 4+2 or 4+1 – *outereloi*-group) (Zaballos & Wrase, 1998; Serrano & Aguiar, 2008). The latter character presents a degree of variability (4+2, 4+3 or 4+1, 4+2, 4+3) within several other *Typhlocharis* groups also (e.g. Zaballos & Pérez-González, 2011; Pérez-González *et al.*, 2013; see also Pérez-González & Zaballos, 2012: table 1).

At a first sight, the absence of a median tooth in clypeus and teeth in the apical margin of elytra allows the inclusion of *T. mendesi* sp. nov. in the *silvanoides*- or *diecki*-group. The former group includes six species (see Serrano & Aguiar, 2014: table 1) and is known for the stability of the 4+4 umbilicate series pattern and the absence of teeth in the apical margin of elytra (see Pérez-González & Zaballos, 2012: table 1). Thus, *T. mendesi* sp. nov. shares with all species of the *silvanoides*-group the absence of teeth in the apical margin of the elytra, but it is well differentiated by the 4+2 umbilicate series pattern. The *diecki*-group includes eleven species (see Serrano & Aguiar, 2014: table 1), all with 4+3 umbilicate series pattern and of which only *T. arnata* Coiffait, 1969 and *T. deferreri* Zaballos & Pérez-González, 2011 present an apical margin of elytra without teeth also (see Pérez-González & Zaballos, 2012: table 1). So, for both the *silvanoides*- and *diecki*-group the 4+2 umbilicate series pattern of the new species is apparently incompatible. This could be solved redefining both groups by encompassing species with 4+2 umbilicate series pattern, which would allow the inclusion of *T. mendesi* sp. nov. in one of them. Taking into account only this pattern of umbilicate series, the new species could be included in some of the remaining groups too.

Thus, apart the difficulty into which species group the new species should be included, it is easily differentiated from all species of the *silvanoides*- or *diecki*-group by the 4+2 umbilicate series pattern and from part of the species of these two groups by the presence of abdominal ‘belt’ in males and females also (see Serrano & Aguiar, 2014: table 1). On the other hand, it is easily differentiated from all species of the *monastica*-group by the female genitalia model (tubular gonocoxite *vs.* unguiform gonocoxite shapes), from the *quadridentata*-group [all species except *T. quadridentata* (Coiffait, 1969)] by the tarsal formula (5+5+5 *vs.* 4+4+4) and the absence of elytral teeth in the apex and from the *gomezi*-, *carpetana*-, *outereloi*- and *baetica*-group – among other traits – by the absence of elytral teeth in the apex (see Pérez-González & Zaballos, 2012: table 1; 2013b: table 1).

However, by the female tubular genitalia model (submodel with long tubular gonocoxites without lateral

setae and two apical nematiform setae) (Pérez-González & Zaballos, 2012), the tarsal formula (5+5+5), the absence of a median clypeal tooth and of meso- and metatibial apical teeth, it seems closer to the *outereloi*-group. This group is characterized by the presence of at least one sutural tooth or yet additional one at the end of the 7th elytral striae. Taking into account the above set of characters, we propose that *Typhlocharis mendesi* sp. nov. must be incorporated in *outereloi*-group. This implies also that the characterization of the group needs to be redefined by the inclusion of ‘absence of teeth in the apical margin of elytra’. This redefinition avoids the creation of a new species group, which would greatly complicate the artificial systematics of the genus.

The *outereloi*-group contains a variety of morphologically diverse species (e.g. Serrano & Aguiar, 2008: table 2; Pérez-González & Zaballos 2012: table 1). Within the group, the new species differs from *T. elenae* Serrano & Aguiar, 2002 and *T. gomesalvesi* Serrano & Aguiar, 2002 by the umbilicate series pattern (4+2 *vs.* 4+1), but shares with 5 species (*T. outereloi* Novoa, 1979, *T. bazi* Ortuño, 2000, *T. laurentii* Magrini, 2000, *T. singularis* Serrano & Aguiar, 2000 and *T. gomesalvesi*) the presence of a *pars stridens* as well as with 3 species (*T. laurentii*, *T. singularis* and *T. gomesalvesi*) the presence of a medial hiatus in the pronotum. Another feature shared by the new species and both sexes of 8 species of the group (*T. outereloi*, *T. bazi*, *T. belenae* Zaballos, 1983, *T. intermedia* Zaballos, 1986, *T. navarica* Zaballos & Wrase, 1998, *T. laurentii*, *T. singularis* and *T. gomesalvesi*) are the ovoid-elongate hind trochanters versus the thorn-shaped (at least in males) in the remaining species. Additionally, the presence of a fovea in the female abdominal sternum II or sterna II and III is shared by 6 species (*T. bazi*, *T. navarica*, *T. atienzai* Zaballos & Ruiz-Tapiador, 1997, *T. estrellae* Zaballos & Ruiz-Tapiador, 1997, *T. bullaquensis* Zaballos & Ruiz-Tapiador, 1997 and *T. elenae*). It seems that morphologically the new species is more akin to *T. singularis*, *T. gomesalvesi*, and *T. laurentii*. Interestingly, the two former species occur geographically closer to Portugal (Serrano & Aguiar, 2000, 2002), and the latter farther away (Almeria, Spain) (Magrini, 2000). Moreover, *T. mendesi* sp. nov. is also similar to *T. laurentii* concerning the number of setae of the female gonocoxite (apical and lateral: 2, 0). However, the new species is easily separated from all species of the *outereloi*-group, including the closely resembling ones, by the absence of teeth in apical margin of elytra and the presence of a slight fovea in the male abdominal sternum II (Figs 6, 7). There are three *Typhlocharis* species belonging to other species groups with a known geographical distribution in Portugal which is closer to the new species than the other two mentioned above (*T. singularis* and *T. gomesalvesi*). They are *Typhlocharis rochapitei* Serrano & Aguiar, 2008, *T. passosi* Serrano & Aguiar, 2005, and *T. bivari* Serrano & Aguiar, 2006, belonging to the *diecki* and *gomezi* species groups,

respectively. *Typhlocharis rochapitei* was found in the same region of the new species (see also the ‘Ecological remarks’) and *T. passosi* and *T. bivari* were located more northerly and far away (60 km) in the region of Serra d’Aire e Candeeiros (Serrano *et al.*, 2005; Serrano & Aguiar, 2006). These observations reinforce the idea that the existing species groups, eventually with the exception of the *baetica*-group (Pérez-González *et al.*, 2013; Pérez-González & Zaballos, 2013c), have no biogeographical or phylogenetic meaning and that obviously many traits that define them are probably convergences (e.g. see Ortuño & Gilgado, 2011).

Despite the above comments, the inclusion of *T. mendesi* sp. nov. based on external morphologic characters in one of the already established species groups nevertheless challenges the relationships of the species so far included in each group.

ECOLOGICAL REMARKS

The new species of *Typhlocharis* inhabit the endogean environment in the same way as other congeneric taxa. They live in the soil, usually at different depths of the B-horizon, but are found also under sunken stones lying at different depths, even from superficial (epigean) to well-buried (edaphic or endogean) environments. Individuals of endogean carabids are more easily found close to the superficial horizon layers after heavy rains because then the soil reaches higher percentage of humidity (saturation or close to saturation), pushing the beetles upwards (e.g. Serrano & Aguiar, 2011; Zaballos & Pérez-González, 2011).

Typhlocharis mendesi sp. nov. was found in three geographically close localities (see description) with calcareous rocky substrate and clayey brown- or brown-red-dish colour soils. The habitats in the Bucelas and Arruda dos Vinhos region are dominated by dense herbaceous vegetation, typical of grassland (e.g. gramineous, liliaceous, leguminous, orchidaceous, asteraceous plants) with holm-oaks (*Quercus ilex* Linnaeus), pine trees (*Pinus pinaster* Aiton), daphnes (*Daphne gnidium* Linnaeus), hawthorns (*Crataegus monogyna* Jacquin), and other woody plants, while in A. do Mourão the vegetation is only grassland. The new species is syntopic with other endogean carabid species in the localities of Bucelas and Arruda dos Vinhos such as *Typhlocharis rochapitei*, *Geocharis olisipensis* (Schatzmayr, 1937), and *Geocharis capelai* Serrano & Aguiar, 2012 and also with other soil endogean arthropods like pseudoscorpionids, zopherid beetles (*Doderonymus lusitanicus* Binaghi, 1937), curculionid beetles, and hymenopteran formicids [*Ponera coarctata* (Latreille, 1802) and *Solenopsis* sp.]. The great concentration of endogean carabid beetles (at least four species) in Bucelas, among other endogean species, confers to this region a statute of a biodiversity ‘hot-spot’. Unfortunately, the region suffers from strong

human influence and threats, like quarry industries, off-road racings, and other activities.

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First record of *Gracixalus quyeti* (Amphibia: Anura: Rhacophoridae) from Laos: molecular consistency versus morphological divergence between populations on western and eastern side of the Annamite Range

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Abstract: We report the first country record of the poorly known *Gracixalus quyeti* from Laos based on a recently collected specimen from Khammouane Province, central Laos. While the genetic analysis revealed nearly identical sequences, we found some differences in body ratios and color patterns among the specimen from Laos and the type series from the eastern side of the Annamite Range in Vietnam.

Keywords: *Gracixalus quyeti* - biogeography - distribution - new record - Annamite Range - Laos.

INTRODUCTION

Although the knowledge of amphibian diversity in Laos has strikingly increased within the last two decades, distribution patterns and natural history of many species are still poorly known (Luu *et al.*, 2014). Information about the geographic distributions of species is essential for understanding their evolution and ecology and is furthermore crucially required for effective conservation (Nguyen *et al.*, 2014; Rowley *et al.*, 2015). The rhacophorid genus *Gracixalus* currently contains 11 species whose ranges are restricted to lowland and montane forests in China, Thailand, Vietnam and Laos (Nguyen *et al.*, 2008; Rowley *et al.*, 2011; Matsui *et al.*, 2015; Frost, 2016). Luu *et al.* (2014) recorded *G. supercornutus* (Orlov, Ho & Nguyen, 2004) from Laos, which also represented the first record of the genus *Gracixalus* from

this country. However, relatively little is known about this genus, and distribution ranges of species within the genus are largely unknown (Luu *et al.*, 2014).

In this study, we report *Gracixalus quyeti*, a recently described and rare species from Phong Nha – Ke Bang National Park (NP) in central Vietnam, for the first time from Hin Nam No National Protected Area (NPA) in central Laos on the western side of the Annamite Range.

MATERIAL AND METHODS

Material examined: A single female specimen of *Gracixalus quyeti* (VNUF A.2014.73) was collected by Vinh Quang Luu, Thomas Calame, Dung Van Phan and Kieusomphone Thanabuaosy during a field survey in May 2014 in Noong Ma Village (17°17.394' N, 106°09.980'

E, 592 m a.s.l., recorded by a Garmin GPSMAP 60CSx GPS receiver and recorded in datum WGS 84), within Hin Nam No NPA, Boualapha District, Khammouane Province, central Laos (Fig. 1).

Sampling methods: The specimen was caught by hand and anaesthetized in a closed vessel with a piece of cotton wool containing ethyl acetate. After taking photographs, the specimen was fixed in 80% ethanol and subsequently transferred into 70% ethanol for permanent storage. A tissue sample was preserved separately in 95% ethanol. The specimen has been deposited in the collection of the Vietnam National University of Forestry (VNUF), Hanoi, Vietnam.

Molecular analysis: Total genomic DNA was extracted from a tissue sample using a commercially available DNeasy Tissue Kit following manufacturer's instructions (QIAGEN Inc., Valencia, CA, USA). A fragment of 16S gene was amplified using the primer pair 16Sar + 16Sbr (Palumbi *et al.*, 1991). The standard PCR conditions used for 16S were: 95° C for 5 min., 40 cycles of [95° C for 30 sec., 50° C for 45 sec., 72° C

for 60 sec.] and 72° C for 6 min. All PCR products were visualized on a gel before sequencing. Successful amplifications were purified to eliminate PCR components using GeneJET™ PCR Purification kit (Fermentas, Canada). Purified PCR products were sent to Macrogen Inc. (Seoul, South Korea) for sequencing. The obtained sequence was compared to those available from other species using the BLAST search in GenBank.

Morphological analysis: Determination of morphological characters followed Nguyen *et al.* (2008). Measurements were taken by the first author with a digital caliper to the nearest 0.1 mm. Abbreviations were used as follows: SVL: snout-vent length; HL: head length (from the back of mandible to the tip of snout); HW: head width (across angle of jaws); MN: distance from the back of mandible to the nostril; MFE: distance from the back of mandible to the front of eye; MBE: distance from the back of mandible to the back of eye; IFE: distance between the front of eyes; IBE: distance between the back of eyes; IN: internasal distance; EN: distance from the front of eye to the nostril; EL: horizontal eye diameter; NS: distance from nostril to the tip of snout; SL: distance from the front of eye to the tip of snout; TYD: greatest tympanum diameter; TYE: distance from tympanum to the back of eye; IUE: minimum distance between upper eyelids; UEW: maximum width of upper eyelid. Forelimb: HAL: hand length (from the base of outer palmar tubercle to the tip of fourth toe); FLL: forelimb length (from the elbow to the base of outer tubercle); TFL: third finger length (from the base of the first subarticular tubercle to the tip of third toe); fd1-4: width of discs of fingers I-IV; fw1-4: width of fingers I-IV (measured at the narrowest point of the distant phalanx). Hindlimb: FL: femur length (from vent to knee); TL: tibia length; TW: tibia width; FOL: foot length (from the base of inner metatarsal tubercle to the tip of fourth toe); FTL: fourth toe length (from the base of the first subarticular tubercle to the tip of fourth toe); TFOL: distance from the base of tarsus to the tip of fourth toe; IMT: length of the inner metatarsal tubercle; ITL: inner toe length; td1-4: width of discs of toes I-IV; fw1-4: width of toes I-IV (measured at the narrowest point of the distant phalanx). Webbing: MTF: distance from the distal edge of metatarsal tubercle to the maximum incurvation of web between third and fourth toes; TTF: distance from the maximum incurvation of web between third and fourth toes to the tip of fourth toe; MTF: distance from the distal edge of metatarsal tubercle to the maximum incurvation of web between fourth and fifth toes; FTF: distance from the maximum incurvation of the web between fourth and fifth to the tip of fourth toe. Webbing formula followed Glaw & Vences (2007). Comparative data were taken from Nguyen *et al.* (2008). Institutional abbreviations are as follows:

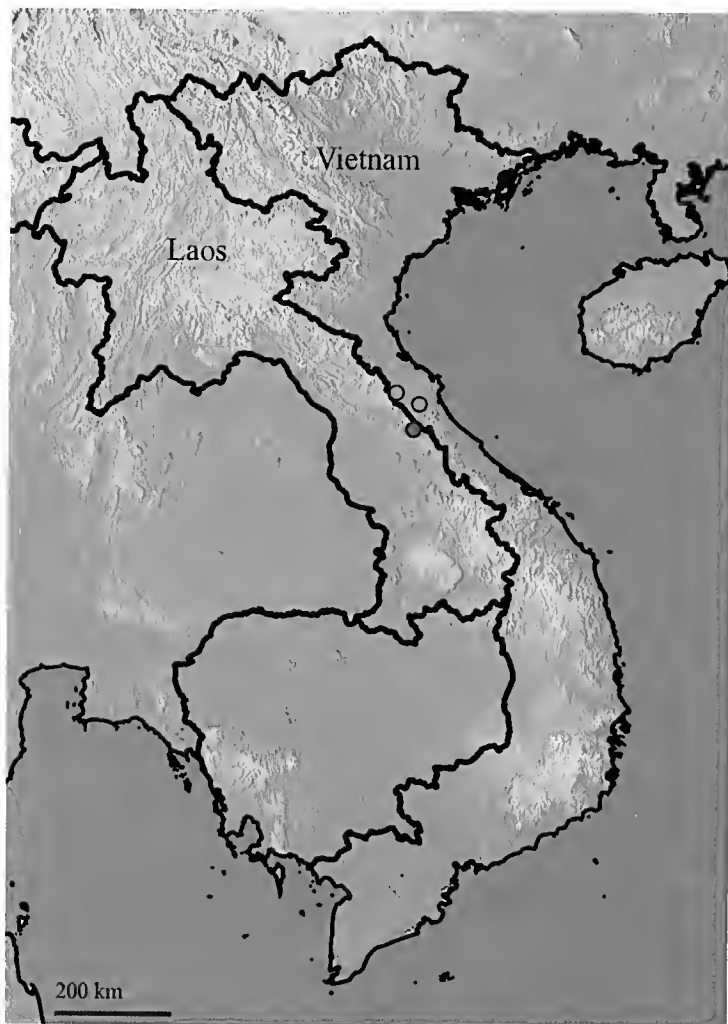


Fig. 1. Map showing the distribution of *Gracixalus quyeti*, including the localities of the type series after Nguyen *et al.* (2008) in Quang Binh Province, Vietnam (marked with blue dots) and our first record from Khammouane Province, Laos (marked with a red dot).

ZFMK: Zoologisches Forschungsmuseum Alexander Koenig, Bonn, Germany; VNUH: Vietnam National University, Hanoi, Vietnam.

RESULTS

Ecology of examined specimen: The Laotian specimen was found at night (20:30) sitting on a branch of a shrub, ca. 0.5 m above an outcrop at an elevation of 592 m above sea level. The air temperature was 27.3°C and the relative humidity was 80%. The locality was surrounded by limestone cliffs and karst vegetation, mainly consisting of species of Ebenaceae, Dracaenaceae, Arecaeae, Meliaceae, and Moraceae.

Molecular analysis: The obtained sequence had 656 bps. Comparative analysis of the obtained sequence with those from GenBank (ZFMK 82999: EU871429.1, VNUH 160706: EU871428.1) showed 99% similarity between the newly collected specimen from Laos (VNUF A. 2014.73) and the holotype (ZFMK 82999) as well as the paratype (VNUH 160706) of *Gracixalus quyeti* from Vietnam. Specifically, the new sequence was different from EU871429.1 in one position and EU871428.1 in two positions.

Morphological analysis: The morphological diagnosis coincided with the original description of *G. quyeti* from central Vietnam (Nguyen *et al.*, 2008) in the following characters: Small rhacophorid (ZFMK 82999 SVL 34 mm, VNUF A. 2014.73 SVL 31.4 mm), vomerine teeth absent. Snout rounded, longer than the diameter of eye. Nostrils closer to tip of snout than to eye. Pupil oval and horizontal. Tympanum distinct, rounded and wider than disc of finger III. Dorsal surface of head and body and upper part of flanks with small sharp tubercles. A dark pattern forming an inverse Y, triangular spot between eyes bifurcating into two bands continuing posteriorly onto the back. Brown marbling on margin of throat and throat. Webbing moderately

developed: Ii(1)-(2)IIe(0.5)-(1 2/3)IIIe(0.5)-(2)IVe(2)-(0.5)iV.

Despite the high genetic correspondence, we also noted some differences in morphology between the examined specimen from Laos and the type specimens of *G. quyeti* (Nguyen *et al.*, 2008): *Body ratios:* Head wider than long, in contrast to longer than wide in the type series. Forelimb and hand length slightly shorter, the latter approximately 27% of SVL (30% in the holotype and 28% in the paratype). Length of finger III approximately 16% of SVL and remarkably shorter than in the specimens from Vietnam (24% in the holotype and 19% in the paratype). Hind limb approximately 1.45 times longer than SVL, shorter than in specimens from Vietnam (holotype: 1.6, paratype: 1.7). Tibia 1.5 times thinner than in the holotype. Length of toe IV 23% of SVL, remarkably shorter than in the holotype (37%) and slightly shorter compared to the paratype (25%) (Tab. 1). *Coloration in life:* Dorsal surface of head and body is greenish beige to grayish light-brown with a grayish dark-brown blotching pattern as described above, in contrast to brownish to moss-green with a dark brown pattern in the adult holotype and moss-green with an indistinct pattern in the subadult paratype. Forelimb and dorsal part of hindlimbs are beige to grayish light-brown with grayish dark-brown bands, versus moss-green with dark brown bands in the holotype and the subadult paratype. The ventral surface can only be described based on the preserved specimen: Belly, chest and throat slightly white to yellowish white with brown marbling on margin of throat and throat, versus background color more yellowish in the preserved holotype and more bluish in the living paratype (Fig. 2A-B).

DISCUSSION

The new record of *Gracixalus quyeti* from Hin Nam No NPA, Laos is approximately 80 km straight line distance apart from the type locality in Quang Binh Province,

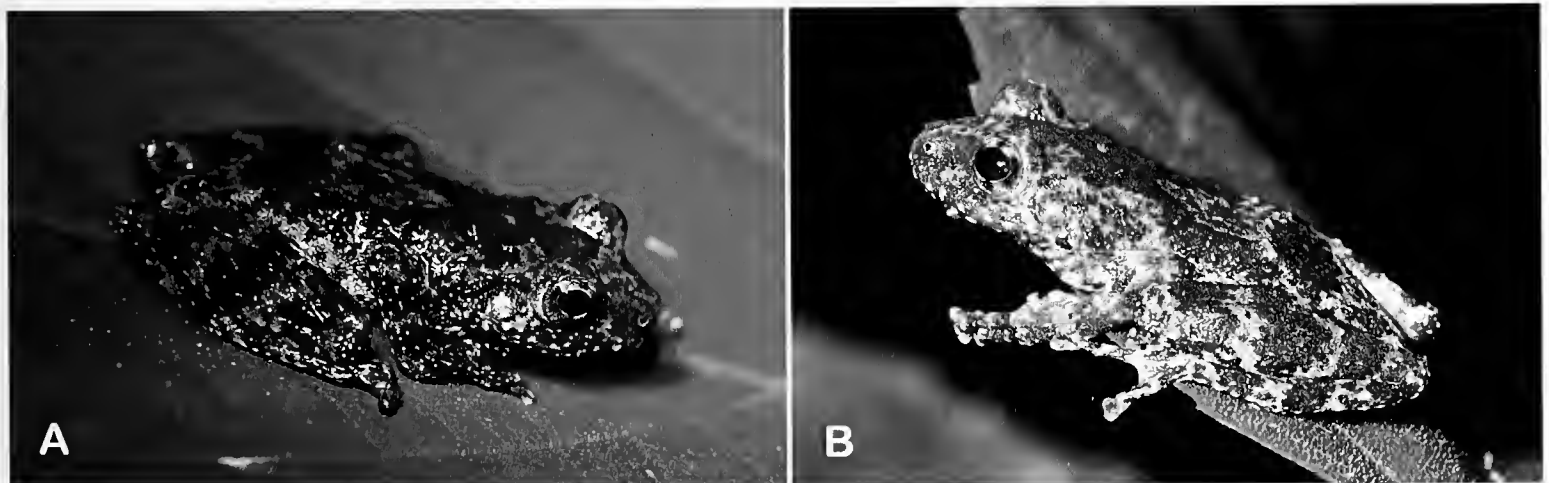


Fig. 2. Female of *Gracixalus quyeti* from Hin Nam No NPA, central Laos. (A) Dorsolateral view. (B) Lateral view. Photos: T. Calame.

Table 1. Morphological characters of the newly collected specimen of *Gracixalus quyeti* from Laos in comparison with the type series from Vietnam (after Nguyen *et al.*, 2008; measurements in mm, abbreviations defined in the text).

	VNUF A. 2014.73	ZFMK 82999	VNUH 160706
	female	female, holotype	subadult, paratype
	Hin Nam No NPA, central Laos	Phong Nha – Ke Bang NP central Vietnam	Phong Nha – Ke Bang NP, central Vietnam
SVL	31.4	34.0	22.0
HL	10.3	12.5	8.2
HW	11.73	11.4	7.4
MN	10.3	11.2	7.4
MFE	6.96	8.4	5.4
MBE	3.86	4.5	3.3
IFE	5.45	6.9	4.3
IBE	8.5	11.0	6.8
IN	3.08	3.0	2.1
EN	2.9	3.5	2.5
EL	4.0	4.8	3.2
NS	1.34	2.1	1.3
SL	4.22	5.4	3.8
TYD	2.0	2.5	1.6
TYE	0.92	1.0	0.7
IUE	3.89	4.1	2.4
UEW	2.36	3.0	1.8
HAL	8.4	10.3	6.1
FLL	6.4	7.2	4.9
TFL	4.97	8.1	4.2
fw 1-4	0.31/0.36/0.38/0.36	0.6/0.9/1/0.9	-
fd 1-4	0.48/0.83/0.99/1	1/1.6/1.9/1.7	1.2 (fd 3)
FL	15.68	18.5	11.5
TL	17.61	20.0	11.8
TW	2.57	4.2	2.0
FOL	12.21	15.2	13.9
FTL	7.1	12.5	5.6
TFOL	20.47	24.8	8.1
IMT	0.82	1.3	0.8
ITL	3.83	4.2	1.9
MTTF	7.1	9.4	3.9
MTFF	7.3	9.8	4.7
TFTF	4.71	5.6	3.0
FFTF	4.38	5.0	2.8
tw 1-5	0.28/0.29/0.36/0.49/0.4	0.8/0.9/1.1/1.3/1.1	-
td 1-5	0.35/0.66/0.6/0.96/0.8	0.5/0.6/0.7/0.9/0.8	-

central Vietnam. It is likely that *G. quyeti* is more widespread across the Annamite’s extensive limestone areas of central Vietnam and central Laos. The species might potentially be endemic to these fragmented lowland and montane forest habitats, while its occurrence seems to be relatively rare within this presumed distribution range.

All records of *G. quyeti* were derived from different elevations in the limestone area within the transition zone between the northern and central Annamite Mountains, a semiconnected array of hills and forested limestone karst outcrops. The Annamite Range generally experiences a tropical wet monsoon climate, while the eastern oceanic Phong Nha – Ke Bang NP receives more precipitation

and has lower average temperatures than Hin Nam No on the western side in the rain shadow of the Annamite Range (Timmins & Trinh 2001; Sterling *et al.*, 2006; Bain & Hurley, 2011). Taking into account the climatic differences between both sides of the Annamite Range and the lack of knowledge about the genus *Gracixalus*, further research must clarify if the shown morphological differences in coloration and body ratios may possibly reflect ecological adaptations to different environments, evolutionary driven morphs or likely just reflect variation within this poorly known species. Still, our finding elevates the number of amphibian species recorded from Laos to 100, and the number of rhacophorid species known to occur in Laos to 34. Although the species number of amphibians known from Laos has nearly doubled during the last 15 years from 58 to 100 recorded species, the amphibian species richness of Laos is still underestimated (Stuart, 1999; Teynié *et al.*, 2014; Luu *et al.*, 2014; Frost, 2016). In particular big gaps remain in our knowledge of the Annamite's amphibian ecology and distribution.

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**The Diplopoda (Myriapoda) of Madagascar described by
Henri de Saussure and Leo Zehntner**

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Abstract: Henri de Saussure and Leo Zehntner described 76 species of millipede in three publications on the fauna of Madagascar (including additions from other islands). These species are listed alphabetically; the holdings of the Muséum d'histoire naturelle de Genève and the whereabouts of type specimens identified in other institutions are discussed, and the currently valid combination is given for each species. *Spirobohus sikorae* is transferred to the genus *Hylekobolus*.

Keywords: Millipedes - Grandidier - Voeltzkow - Sikora - Geneva - Paris - type catalogue.

INTRODUCTION

The early Diplopoda collections of the Muséum d'histoire naturelle de Genève (MHNG) were greatly enriched by the material brought back from the expeditions of Henri de Saussure to Mexico and the Antilles in 1854-1856 and of Aloïs Humbert to Sri Lanka (then Ceylon) in 1858-1860.

Saussure published accounts of the species he had collected on his expedition (Saussure, 1859a, b, 1860). Humbert also published a monograph on the species he had collected (Humbert, 1865). They then collaborated on further publications, concentrating primarily on the fauna of the Americas (Humbert & Saussure, 1869a, b, 1870; Saussure & Humbert, 1872). Late in his career, assisted by Leo Zehntner, Saussure returned to the Myriapoda to bring Humbert's unfinished monograph on the Diplopoda of the Geneva region to publication (Humbert, 1893). Zehntner had been engaged as assistant in the MHNG in 1890, working there for four years. He returned for six months in 1900 to work as Saussure's personal assistant and went on to have a distinguished career as an applied entomologist in Java and Brazil (Hauser, 1972).

It was presumably this resumption of interest in the group that led to Saussure being asked to study the material collected for Grandidier's Madagascar series (associated with Muséum national d'Histoire naturelle in Paris) and by Voeltzkow's expedition to that island (associated with the Senckenberg Naturmuseum, Frankfurt). Since these publications form a distinct entity in both faunistic and stylistic terms, they are here considered first, and an

account of Humbert and Saussure's earlier works will be published elsewhere. In the publications considered here Saussure and Zehntner described 76 species of millipede, nearly all from Madagascar, the few exceptions coming from Zanzibar and the Seychelles.

Saussure & Zehntner's Madagascar publications are often cited with the date 1902 (see Krabbe, 1982 for example) but are actually three publications with different dates (Jeekel, 1971). The article on Voeltzkow's expedition (Saussure & Zehntner, 1901) appeared in September 1901 even though the fascicle in which it was published bears the date 1902. The first twelve plates associated with the volume in Grandidier's Madagascar series were published in 1897 and represent the first valid publication of the species names although not accompanied by a description (Saussure & Zehntner, 1897). The last three plates (13-15) appear to have been published together with the text (Saussure & Zehntner, 1902), contrary to the information on the title page preceding the plates which was also delivered with the text in 1902.

Many of the specimens are accompanied by identification labels giving only limited locality information; in many cases there are two such labels, one in pencil, in the handwriting of Zehntner or Jean Carl (MHNG assistant, curator and then assistant director between 1900 and 1943, and a distinguished Diplopoda taxonomist in his own right). Given that the labels appear to be contemporary with the descriptions, specimens with such labels are presumed to be types even if this is not explicitly stated on the label.

The nomenclature generally follows Enghoff (2003); changes made in subsequent revisions are mentioned in the text. The generic placement of some names remains uncertain and we follow Enghoff in placing some genus names in inverted commas or with a question mark.

ARRANGEMENT AND FORMAT

The species are listed alphabetically. The format for each is:

specific epithet Author, publication: page [*Original generic placement*].

Provenance as given in the original description, depository. Type series.

Number of specimens in the MHNG, label data of type specimens. Type specimens identified in other collections. Other information.

Currently valid combination

The following abbreviations are used in the list:

BMNH The Natural History Museum, London

MHNG Muséum d'histoire naturelle de Genève

MNHN Muséum national d'Histoire naturelle, Paris

NHMW Naturhistorisches Museum, Vienna

SMF Senckenberg Naturmuseum, Frankfurt

TW Thomas Wesener

The specimens in the MNHN have two series of specimen identification numbers; those in the online database that have the prefix MY and those previously applied in the collections that have the prefix CB, HC or HB. These are both cited where we have both numbers.

CATALOGUE

alluandi Saussure & Zehntner, 1902: 58-60, pl. 15, fig. 8 [*Sphaerotherium*].

Madagascar. Fort Dauphin (leg. Alluaud, Musée de Paris). Unspecified number of ♂ and ♀.

The MHNG collection contains one ♀ specimen in alcohol under the name *Sphaerotherium alluandi*. The identification labels have only "Madagascar" for the locality but the specimen is probably part of the type series. A ♂ specimen in the MNHN was designated as lectotype by Wesener & Sierwald (2005a: 8). There are also two ♀ paralectotypes in the MNHN (MNHN CB006/MY2925).

Zoosphaerium alluandi (Saussure & Zehntner, 1902)

ambulator Saussure & Zehntner, 1897: pl. 7, fig. 8, pl. 9, fig. 31 [*Spirostreptus*].

Illustration without description.

Saussure & Zehntner (1902: 243-246, pl. 14, fig. 12) gave a description of both sexes and the locality information "Madagascar. Robillard (Musée de Genève), M. Catat

(Muséum de Paris), Province d'Imerina (Sikora)." They also mention a specimen from Mauritius as a variety, but this should not be considered a syntype. The MHNG collection contains four specimens in alcohol in two jars under the name *Spirostreptus amubulator*. Both jars contain identification labels with "Madagascar" written on them. The jar with two ♂ and one ♀ also contains a tube with dissected parts including gonopods and the label "Sph. ambulator n." All of these specimens are presumably syntypes. The specimen from Mauritius, also stated to be in the MHNG in the original description could not be found. According to Krabbe (1982) there is type material in the MNHN, but the species is not listed in their online database.

A junior synonym of *Sechelleptus argus* (Attems, 1896)

anale Saussure & Zehntner, 1897: pl. 4, fig. 4 [*Sphaerotherium*].

Illustration without description.

Saussure & Zehntner (1902: 30-32) gave the description of the ♀ and the locality information "Antananarivo (British Museum, 2 ♀ adultes et des jeunes)." They also reported a ♀ from "Madagascar. Côte Sud-Ouest (Alfred Grandidier)." No specimens found in the MHNG. As the specimens from the BMNH are considered lost, the female specimen from the MNHN (MNHN CB007/MY2917) was selected as the lectotype by Wesener & Wägele (2008: 76).

Zoosphaerium anale (Saussure & Zehntner, 1897)

anomalum Saussure & Zehntner, 1902: 56, pl. 15, fig. 7 [*Sphaerotherium*].

Madagascar. Isaka (Muséum de Paris, récolté par M. Alluaud). One ♂.

No specimens found in the MHNG. The holotype is in the MNHN (MNHN CB009/MY2919) according to their online database and Wesener & Wägele (2008).

Zoosphaerium anomalum (Saussure & Zehntner, 1902)

antimena Saussure & Zehntner, 1901: 453-454, fig. 33 [*Spirostreptus*].

Insulis Nossibé et Sacatia leg. Voeltzkow. One broken ♂ and an unspecified number of ♀.

The MHNG collection contains two specimens in alcohol under the name *Spirostreptus antimena*. There is no data label but the identification labels have "Madagascar, Dr Voeltzkow" written on them, indicating that they are syntypes. There is also a vial with dissected gonopods in the jar. According to Krabbe (1982) there is type material in the SMF but their online database does not list this species.

Eumekius antimena (Saussure & Zehntner, 1897)

betaminea Saussure & Zehntner, 1897: pl. 10, fig. 38 [*Spirostreptus*].

Illustration without description.

Saussure & Zehntner (1902: 274-276) gave a description of both sexes and the locality information "Madagascar.

Antananarivo (Sikora)". The MHNG collection contains parts of at least three specimens in alcohol under the name *Spirostreptus betaminena*. There is no data label, but the identification labels have "Madagascar" written on them. There is also a vial with the dissected gonopods of two specimens and the label "*Spirostreptus betaminena* S + Z ♂." These specimens are presumably syntypes.

Sechelleptus betaminena (Saussure & Zehntner, 1897)

betsilea Saussure & Zehntner, 1897: pl. 10, fig. 43 [*Spirostreptus*].

Illustration without description.

Saussure & Zehntner (1901: 455-456, figs 47-49) gave a description of both sexes and the locality information "Madagascar occidentalis, Mayunga leg. Voeltzkow (Musée de Genève)". Saussure & Zehntner (1902: 263) stated that the specimens were deposited in the MHNG. The MHNG collection contains parts of at least three specimens in alcohol under the name *Spirostreptus betsileus*. There is no data label but the identification labels have "Madagascar occident." written on them. There is also a vial with dissected gonopods in the jar. These specimens are presumably all syntypes.

Charactopygus betsilea (Saussure & Zehntner, 1897)

bicolor Saussure & Zehntner, 1902: 227, pl. 15, fig. 14 [*Spirostreptus*].

There is no description to accompany the illustration, and in the text the name is simply presented as a junior synonym of *Spirostreptus fulgens* Saussure & Zehntner, 1901 before the description of the species. This strongly suggests that the plate was created some time before it was published in 1902. There are no specimens under this name in the MHNG.

A junior synonym of *Sechelleptus fulgens* (Saussure & Zehntner, 1901)

bivalvis Saussure & Zehntner, 1897: pl. 7, fig. 17 [*Spirostreptus*].

Illustration without description.

Saussure & Zehntner (1902: 192-194) gave a description, the locality information "Madagascar. (leg. Dr Keller, musée de Genève)" and stated that they had one ♀. No specimens found in the MHNG. The whereabouts of the holotype is unknown. Considered a nomen dubium by Krabbe (1982). The generic placement is uncertain.

"*Spirostreptus*" *bivalvis* Saussure & Zehntner, 1897

blandum Saussure & Zehntner, 1902: 63-65, pl. 15, figs 9-10 [*Sphaerotherium*].

Madagascar. Col de Sakavalana (Muséum de Paris, Alluaud), Andrahomana. Three ♂.

The MHNG collection contains one specimen in alcohol under the name *Sphaerotherium blandum*. Both of the identification labels in the jar have "Madagascar" written on them. The jar also contains a vial with dissected telopods and the label "Sph. blandum n." indicating

that the specimen is part of the type series. According to their online database the MNHN have the two syntypes collected by Alluaud (MY2921 and MY2922); the mature male at the MNHN (CB011) was referred to as the holotype and the immature male as paratype by Wesener & Wägele (2008: 63); the male used for their redescription was designated as lectotype by Wesener (2016: 83).

Zoosphaerium blandum (Saussure & Zehntner, 1902)

caelebs Saussure & Zehntner, 1897: pl. 2, fig. 7, pl. 9, fig. 27 [*Spirostreptus*].

Illustration without description.

Saussure & Zehntner (1902: 255-258) gave the description of the ♂, stating that they had one immature specimen, and the locality information "Madagascar (Muséum de Paris)". No specimens found in the MHNG. According to Krabbe (1982) the holotype is in the MNHN, but it is not listed in their online database. Considered a nomen dubium by Krabbe (1982). The generic placement is uncertain.

"*Spirostreptus*" *caelebs* Saussure & Zehntner, 1897

campanulatum Saussure & Zehntner, 1897: pl. 4, fig. 6 [*Sphaerotherium*].

Illustration without description.

Saussure & Zehntner (1902: 28-30) gave a description and the locality information "Madagascar. Côte Sud-Ouest (Alfred Grandidier 1 ♂)". The MNHN online database lists the holotype (MY2926). The MHNG collection contains a card mount associated with the label "Sphaerotherium campanulatum S & Z ♂ Madagascar" but the mount has a ♀ second pair of legs showing the vulvas, and is clearly not part of the type series.

Zoosphaerium campanulatum (Saussure & Zehntner, 1897)

collaris Saussure & Zehntner, 1897: pl. 11, fig. 45 [*Spirobolus*].

Illustration without description.

Saussure & Zehntner (1902: 119-121), placing the species in the genus *Rhinocricus*, gave a description of the ♀ and the locality information "Madagascar, 3 ♀ récoltées par A. Grandidier (Muséum de Paris)." However, the original description gives measurements for four individuals. The MHNG collection contains one pinned specimen under the name *Rhinocricus collaris*. This specimen has the labels "Madagascar, Grandidier", "Spirobolus collaris S & Z ♀" and "No=39" indicating that it is a syntype. The MNHN has two female syntype specimens (Wesener *et al.*, 2009b: 119) under the number MNHN HB015. The genus *Rhinocricus* is the type genus of the family Rhinocricidae, a family never subsequently recorded from Madagascar (Marek *et al.*, 2003). As all known specimens are females, the real generic and family placement of this species remains uncertain.

"*Rhinocricus*" *collaris* (Saussure & Zehntner, 1897)

colossus Saussure & Zehntner, 1897: pl. 7, fig. 9, pl. 10, fig. 39 [*Spirostreptus*].

Illustration without description.

Saussure & Zehntner (1902: 240-243) gave a description of the ♀ and the locality information "Madagascar. Une seule femelle capturée sur la côte Ouest de l'île par Alfred Grandidier." No specimens found in the MHNG. According to Krabbe (1982) the holotype is in the MNHN but it is not listed in their online database. Considered a nomen dubium by Krabbe (1982). The generic placement is uncertain.

"*Spirostreptus*" *colossus* Saussure & Zehntner, 1897

convolutus Saussure & Zehntner, 1897: pl. 2, fig. 10, pl. 6, fig. 3 [*Spirostreptus*].

Illustration without description.

Saussure & Zehntner (1901) gave a description of both sexes and the locality information "Madagascar (Grandidier et Voeltzkow)". The MHNG collection contains two specimens (one ♂ and one ♀) in alcohol under the name *Spirostreptus convolutus*. One of the identification labels reads "Spirostreptus convolutus Sss. et Zt., Type!, Madagascar, Dr Voeltzkow leg." indicating that they are syntypes. The Grandidier specimen(s) are presumably in the MNHN but are not listed in their online database. No specimens are listed in the SMF online database.

A junior synonym of *Sechelleptus pyrhoronus* (Gerstäcker, 1873)

coquerelianum Saussure & Zehntner, 1897: pl. 1, fig. 2, pl. 5, fig. 11, [*Sphaerotherium*].

Illustration without description.

Saussure & Zehntner (1902: 42-45, pl. 15, fig. 1) gave a description and the locality information "Madagascar. (Muséum de Paris, 2 ♀ de grande taille, 1 ♀ and 2 ♂ moins grand, collectés par Coquerel)" for the type series. After the description they also discussed a number of smaller or damaged specimens, including some in the MHNG, but these probably cannot be considered syntypes. The MHNG collection contains four pinned specimens and two in alcohol under the name *Sphaerotherium coquerelianum*. The pinned specimens are accompanied by a card mount with one the ♀ second pair of legs showing the vulva, glued to it and "Sphaerotherium coquerelianum, ♀ 2° piece" written on it. The leg is much too large to be associated with the specimens present and must be part of one of the syntypes. The other dry specimens are probably amongst the small specimens mentioned but not syntypes. The identification labels in the jar have "Madagascar" written on them and these specimens may be part of the type series. The material at the MNHN contained six ♂ type specimens (MNHN CB034), one of which was selected as a lectotype by Wesener & Wägele (2008: 22). Additional material at the MNHN that was potentially part of the type series are one ♂ and eight ♀ (MNHN CB035) all leg. Grandidier (n°

217), and one ♂ and one ♀ (MNHN CB036), all of these specimens having been labelled in the same handwriting. *Zoosphaerium coquerelianum* (Saussure & Zehntner, 1897)

corallipes Saussure & Zehntner, 1902: 143-146, pl. 15, fig. 3 [*Spirobolus*].

Madagascar. Fort Dauphin (Muséum de Paris, M. Ch. Alluaud). Three ♂ and one ♀.

The MHNG collection contains one specimen in alcohol under the name *Spirobolus corallipes*. One of the identification labels has the locality "♂ Madagaskar Fort Dauphin" written on it, indicating that it is part of the type series. There is a vial with dissected parts including gonopods in the jar. There is a label indicating that the specimen was studied by Hoffman, and that he identified the genus as *Aphistogoniulus*. Wesener *et al.* (2009a: 36) designated a ♂ in the MNHN as lectotype, and one ♀ and one immature as paralectotypes (MNHN HB020).

Aphistogoniulus corallipes (Saussure & Zehntner, 1902)

coriaceus Saussure & Zehntner, 1901: 450, fig. 34 [*Spirostreptus*].

Insula Nossibé, lectus Voeltzkow. Unspecified number of ♂ and ♀.

Saussure & Zehntner (1902: 215-217, pl. 14, fig. 11) gave the same information. The MHNG collection contains two specimens in alcohol under the name *Spirostreptus coriaceus*. There is no data label but the identification labels have "Nosibé" written on them and the specimens are presumably syntypes. The MNHN online database lists two syntypes (MY1829), although the specimens are reported to have been collected by Grandidier. According to Krabbe (1982) there are type specimens in the SMF, although these are not listed in their online database.

Sechelleptus coriaceus (Saussure & Zehntner, 1901)

curvicauda Saussure & Zehntner, 1897: pl. 8 fig. 24 [*Spirobolus*].

Illustration without description.

Saussure & Zehntner (1902: 126) placed this name in synonymy with *S. urophorus* Pocock, 1893. They state that the illustrations were based on three ♀ collected by Lantz in the Seychelles and deposited in the MNHN. Nevertheless, the MHNG collection contains one specimen in alcohol under the name *Spirobolus urophorus* with two identification labels that indicate that it is a syntype of *S. curvicauda*. The MNHN online database lists one specimen (MY9803) which is presumably another syntype although not explicitly stated to be one. A junior synonym of *Eucarlia urophorus* (Pocock, 1893)

dauphini Saussure & Zehntner, 1902: 228-230, pl. 15, fig. 15 [*Spirostreptus*].

Madagascar. Fort Dauphin (M. Alluaud). Unspecified number of ♂ and ♀.

The MHNG contains one specimen in alcohol under the

name *Spirostreptus dauphini*. There is no data label, but one of the identification labels has “Madagascar, Fort Dauphin” written on it, indicating that it is a syntype. There is also a vial containing the gonopods in the tube. According to Krabbe (1982) there are type specimens in the MNHN but their online database does not list this species.

Sechelleptus dauphini (Saussure & Zehntner, 1902)

digitale Saussure & Zehntner, 1897: pl. 5, fig. 16 [*Sphaerotherium*].

Illustration without description.

Saussure & Zehntner (1902: 55-56) give the description of the ♂ and the locality information “Madagascar. Tananarive (Muséum de Paris, M. Catat).” No specimens found in the MHNG. The MNHN have a ♂ specimen (MNHN CB019) referred to as the holotype by Wesener & Wägele (2008: 10).

A junior synonym of *Zoosphaerium neptunus* (Butler, 1872)

dorsopunctatus Saussure & Zehntner, 1901: 441-442, figs 12-13 [*Spirobolus*].

Insula Nossibé. Fragments of unspecified number of ♂ and ♀.

No specimens found in the MHNG. The whereabouts of the type specimens is unknown. Shelley & Lehtinen (1999) placed this name in synonymy with the common tropical tramp species *Trigoniulus corallinus* (Gervais). A junior synonym of *Trigoniulus corallinus* (Gervais, 1841)

dorsovittatum Saussure & Zehntner, 1901: 446-447, figs 28-32 [*Pygodon*].

Ile Nossibé, récoltés par le Dr A. Voeltzkow. Two ♂ and two ♀.

Saussure & Zehntner (1902: 167-170; pl. 13, fig. 7) gave the similar information but did not specify the number of specimens. The MHNG collection contains two specimens in alcohol under the name *Pygodon dorsovittatus*. There is no data label but the identification labels in the jar have “Nosibé, Voeltzkow” written on them, indicating that they are part of the type series. The head, several segments and the gonopods of the ♂ are in a vial in the jar. Wesener & Enghoff (2009: 85) designated the ♂ as lectotype and the ♀ as paralectotype.

Spiromimus dorsovittatus (Saussure & Zehntner, 1901)

exaratus Saussure & Zehntner, 1902: 279, pl. 15, fig. 18 [*Spirostreptus*].

Madagascar, sommet de Ivohitsombé. Ch. Alluaud, Muséum de Paris. One immature ♂.

No specimens found in the MHNG. According to Krabbe (1982) the holotype is in the MNHN, but it is not listed in their online database. Considered a nomen dubium by Krabbe (1982). The generic placement is uncertain.

“*Spirostreptus*” *exaratus* Saussure & Zehntner, 1902

fangaroka Saussure & Zehntner, 1901: 452-453, fig. 35 [*Spirostreptus*].

Insula Nossibé, leg. Voeltzkow. Unspecified number of ♂ and ♀.

The MHNG collection contains parts of at least two specimens in alcohol under the name *Spirostreptus fangaroka*. The specimens are together in a vial, and there is a second vial containing gonopods in the jar. The two identification labels in the jar have the localities “Madagascar” or “Nosibé” written on them, and the specimens are presumably syntypes. According to Krabbe (1982) there is type material in the NHMW.

Isophyllostreptus fangaroka (Saussure & Zehntner, 1901)

fraternum Saussure & Zehntner, 1897: pl. 5, fig. 10 [*Sphaerotherium*].

Illustration without description.

Saussure & Zehntner (1902: 50-51) gave a description of the ♀, stating that they had one specimen, and the locality information “Madagascar (Muséum de Paris, M. Catat).” No specimens found in the MHNG. According to their online database and Wesener & Wägele (2008: 71) the holotype is in the MNHN (CB024/MY2940). The name is a junior homonym of *S. fraternum* Butler, 1872 and has therefore been replaced.

Zoosphaerium fraternarium Jeekel, 1999 (replacement name)

fulgens Saussure & Zehntner, 1897: pl. 10, fig. 40 [*Spirostreptus*].

Illustration without description.

Saussure & Zehntner (1901: 449; fig. 37) gave a description of the ♀ and the locality information “Madagascar occidentalis (Dr Voeltzkow)”. The MHNG collection contains three specimens in alcohol under the name *Spirostreptus fulgens*. One of the identification labels has “♀ Madagascar” written on it, but the other has “♂♀ Madagascar” and the jar also contains two vials with dissected parts; one with gonopods, the other with a gnathochilarium (which was mentioned in the description as the Unterlippe). It is probable that the ♀ specimen with dissected mouthparts is a syntype. According to Krabbe (1982) there is type material in the SMF, but it is not listed in their online database.

Sechelleptus fulgens (Saussure & Zehntner, 1897)

globiclunus Saussure & Zehntner, 1897: pl. 7, fig. 13 [*Spirostreptus*].

Illustration without description.

Saussure & Zehntner (1902: 227-228) gave a description of the ♀ and the locality information “Madagascar. Alfred Grandidier (Muséum de Paris).” No specimens found in the MHNG.

According to Krabbe (1982) there is type material in the MNHN, but this is not listed in their online database. Considered a nomen dubium by Krabbe (1982). The generic placement is uncertain.

“*Spirostreptus*” *globiclunus* Saussure & Zehntner, 1897

globulus Saussure & Zehntner, 1897: pl. 4, fig. 3 [*Sphaerotherium*].

Illustration without description.

Saussure & Zehntner (1902: 34-36) gave a description of the ♂ and the locality information “Nosy Bé (Muséum de Paris).” The MHNG collection contains one specimen in alcohol under the name *Sphaerotherium globulus*. There is also a vial containing the ends of the telopods in the jar. Both identification labels in the jar have “♂ Nosibé” written on them, indicating that the specimen is a syntype. The MNHN has one ♂ specimen (MNHN CB025/MY2941), that was identified as conspecific with *Z. voeltzkowianum* (Saussure & Zehntner, 1897) by Wesener & Wägele (2008: 43), and designated as lectotype by Wesener (2016: 83).

A junior synonym of *Zoosphaerium voeltzkowianum* (Saussure & Zehntner, 1897)

grandidieri Saussure & Zehntner, 1897: pl. 9, fig. 33 [*Spirobolus*].

Illustration without description.

Saussure & Zehntner (1902: 141-143) gave a description of both sexes and the locality information “Madagascar. 1 ♂ jeune et 2 ♀ récoltés par M. Grandidier”. The MHNG collection contains parts of two specimens in alcohol under the name *Spirobolus grandidieri*. Both identification labels have “♂♀ Madagascar” written on them, and there is also a printed label reading “TYPE”, indicating that they are syntypes. The MNHN has one ♀ specimen labelled “type” (MNHN HC001).

Spirobolus (*Trigoniulus*) *grandidieri* Saussure & Zehntner, 1897

grandidieri Saussure & Zehntner, 1897: pl. 10, fig. 41 [*Spirostreptus*].

Illustration without description.

Saussure & Zehntner (1902: 232-234) gave a description of the ♀, stating that they had one specimen, and the locality information “Madagascar. Alfred Grandidier.” No specimens found in the MHNG. According to Krabbe (1982) the holotype is in the MNHN, but it is not listed in their online database.

A junior synonym of *Seychelleptus pyrhoneus* (Gerstäcker, 1873)

hova Saussure & Zehntner, 1897: pl. 5, fig. 23 [*Polydesmus*].

Illustration without description.

Saussure and Zehntner (1901: 436-437) placed the species in the subgenus *Polydesmus* (*Pterodesmus*), gave a cursory description and the locality information “Nossibé”. Saussure & Zehntner (1902: 91-93) placed the species in the subgenus *Polydesmus* (*Tubercularium*), and gave a description of both sexes and the locality “Madagascar (Sikora) 1 ♀ et plusieurs ♂. D’autres ♀ de Nossibé récoltées par le docteur Voeltzkow”. Since the original illustrations of 1897 included ♂ characters, the

specimens collected by Sikora must be part of the type series. The MHNG collection contains six specimens in alcohol in two jars under the name *Tubercularium hova*. The identification labels in the first jar, with four specimens in three vials, have “Madagascar (Sikora)” written on them. The identification labels in the second jar, with two specimens in separate vials, have “Nossibé, Dr Voeltzkow” written on them. These specimens are all syntypes. Golovatch & Hoffman (1989) refer to syntypes in the SMF, but these are not listed in the SMF online database.

Dalodesmus hova (Saussure & Zehntner, 1897)

hova Saussure & Zehntner, 1897: pl. 11, fig. 44 [*Spirobolus*].

Illustration without description.

Saussure & Zehntner (1902: 146-150) gave a description of both sexes and the locality information “Madagascar. Divers ♂ and 1 ♀ récoltés par M. Grandidier. D’autres mâles récoltés par M. Lanz et par M. Catat (Muséum de Paris). The MHNG collection contains four specimens in alcohol in two jars under the name *Spirobolus hova*. One contains one specimen and a vial containing the gonopods. The identification labels have “♂ Madagascar” written on them, and there is a separate label reading “Type.” This specimen is presumably one of the type series. There is also a label indicating that Hoffman studied the specimen and considered that the specimens belonged to the genus *Aphistogoniulus*. The other jar contains much more recently collected and identified specimens which are obviously not part of the type series. Wesener *et al.* (2009: 34) designated a ♂ specimen in the MNHN as lectotype.

Aphistogoniulus hova (Saussure & Zehntner, 1897)

hova Saussure & Zehntner, 1897: pl. 4, fig. 7, pl. 7, fig. 11 [*Spirostreptus*].

Illustration without description.

Saussure & Zehntner (1901: 454-455, figs 43-46) gave a description of the ♂ and the locality information “Madagascar (Sikora); Nossibé (Voeltzkow).” The MHNG collection contains five specimens in alcohol in two jars under the name *Spirostreptus hova*. One jar, containing three specimens, has “Nossibé, Dr Voeltzkow” written on the identification labels, indicating that they are syntypes. The other contains an identification label indicating that the specimens were determined by Carl and are thus not part of the type series. According to Krabbe (1982) there is type material in the SMF but it is not listed in their online database.

A junior synonym of *Charactopygus atratus* (Karsch, 1881)

imbecillum Saussure & Zehntner, 1897: pl. 5, fig. 20 [*Sphaerotherium*].

Illustration without description.

Saussure & Zehntner (1902: 60-61) gave a description

of both sexes and the locality information “Nosy Bé (Muséum de Paris).” The MHNG collection contains two specimens in alcohol under the name *Sphaerotherium imbecillum*. The jar also contains a vial with the ends of the telopods and a label “*Sphaerotherium imbecillum* Sss. & Z. ♂”. Both identification labels in the jar have only “Madagascar” written on them, but there is no reason to suppose that these are not syntypes. There are two ♂ syntypes in the MNHN (MNHN CB031). This name, together with *Z. globulus*, was placed as a junior synonym of *Z. voeltzkowianum* by Wesener & Wägele (2008: 43); the MNHN specimen used for their redescription was designated as lectotype by Wesener (2016: 83).

A junior synonym of *Zoosphaerium voeltzkowianum* (Saussure & Zehntner, 1897)

labialis Saussure & Zehntner, 1897: pl. 10, fig. 42 [*Spirostreptus*].

Illustration without description.

Saussure & Zehntner (1902: 268-269) gave a description of the ♀ and the locality information “Nosy Bé. Espèce récoltée par M. Humblot (Muséum de Paris).” The number of specimens is not given, but in discussing the variation they mentioned “les petits individus” indicating more than one. The MHNG collection contains two specimens in alcohol under the name *Spirostreptus labialis*. The identification labels in the jar have “Nosibé” written on them and the specimens are presumably syntypes. According to Krabbe (1982) there is type material in the MNHN, but this is not listed in their online database. Considered a nomen dubium by Krabbe (1982). The generic placement is uncertain.

“*Spirostreptus*” *labialis* (Saussure & Zehntner, 1897)

leprosus Saussure & Zehntner, 1897: pl. 7, fig. 14 [*Spirostreptus*].

Illustration without description.

Saussure & Zehntner (1902: 239-240) gave a description of the ♀ and the locality information “Madagascar. Fianarantsoa, 1 ♀ et un second individu incomplet (Musée de Genève).” No specimens found in the MHNG. The whereabouts of the type specimens is unknown. This is not *S. leprosus sensu* Attems (1914) who, according to Jeekel (1999), misidentified a specimen of *S. macilentus*. *Sechelleptus leprosus* (Saussure & Zehntner, 1897)

libidinosum Saussure & Zehntner, 1897: pl. 4, fig. s, pl. 15, fig. 2 [*Sphaerotherium*].

Illustration without description.

Saussure & Zehntner (1902: 69-72) gave a description and stated that they had several specimens of both sexes from “Madagascar, collectés par Alfred Grandidier, par Coquerel (Muséum de Paris) et par Sikora (Musée de Genève)” as well as some immature specimens “de la côte occidentale récoltés par M. Voeltzkow.” The MHNG collection contains nine pinned specimens. The six larger specimens have a label reading “Madagascar” on the pin,

and one ♂ and one ♀ have identification labels. They are accompanied by two card mounts, one with telopods glued to it, the other with a ♀ second pair of legs, each with an identification label. The three smaller specimens are each labelled “WEST MADAGASC.” and “VOELTZKOW” and have identification labels. One ♂ has a card mount on the pin with the telopods glued to it and one ♀ has a card mount on the pin with the second pair of legs glued to it. There is a third card mount with a ♀ second pair of legs glued to it and an identification label, but it is not clear which specimen this belongs with. There are also ten specimens in alcohol in two jars under the name of *Sphaerotherium libidinosum*. One jar with four specimens has “Madagascar” written on the identification labels. The other with seven specimens, one separated in a vial, a vial containing parts of a pair of telopods, also has “Madagascar” written on the identification labels. All of these specimens are presumably part of the type series. There are also a number of more recently collected and identified specimens in alcohol under the name *Zoosphaerium libidinosum*; these are clearly not part of the type series. The MNHN online database lists 13 syntypes in three lots (MY2965, MY2966 and MY2969), one ♂ (MNHN CB034) was selected as the lectotype by Wesener & Wägele (2008: 22), while five other ♂ became paralectotypes. Two additional vials (MNHN CB035 & 036) with one ♂ and eight ♀ and one ♂ and one ♀, respectively, were also determined as paralectotypes.

Zoosphaerium libidinosum (Saussure & Zehntner, 1897)

macilentus Saussure & Zehntner, 1897: pl. 6, fig. 4 [*Spirostreptus*].

Illustration without description.

Saussure & Zehntner (1902: 220-222) gave a description of the ♂ and the locality information “Ile Maurice. Robillard (Musée de Genève).” The MHNG collection contains one specimen in alcohol under the name *Spirostreptus macilentus*. The jar also contains a vial with the gonopods in it. One of the identification labels has “Ile Maurice” written on it and the other has “Madagaskar.” It seems likely that the latter is a *lapsus calami* and that the specimen is a syntype.

Sechelleptus macilentus (Saussure & Zehntner, 1897)

madecassus Saussure & Zehntner, 1897: pl. 3, fig. 1, pl. 4, fig. 12 [*Spirostreptus*].

Illustration without description.

Saussure & Zehntner (1902: 252-255) gave a description of both sexes and the locality information “Madagascar. 1 ♂ récolté par le Dr Coquerel; 2 ♀ des Iles Seychelles de très grande taille, récoltées par Rousseau (Muséum de Paris).” No specimens found in the MHNG. According to Krabbe (1982) the type material is in the MNHN, but it is not listed in their online database.

A junior synonym of *Sechelleptus seychellarum* (Desjardins, 1835)

malagassum Saussure & Zehntner, 1897: pl. 6, fig. 2 [*Polyzonium*].

Illustration without description.

Saussure & Zehntner (1902: 285-287) gave a description of both sexes and the locality information “Madagascar. Plusieurs ♀ et un ♂ récoltés par A. Grandidier (Muséum de Paris). Nosy Bé. Une ♀ capturée par le docteur Voeltzkow”. The MHNG collection contains three ♀ specimens in alcohol (currently on loan) under the name *Polyzonium malagassum*. These specimens are presumably part of the type series. According to their online database there are types (one ♂ and five ♀; MY2843) in the MNHN; the ♂ was selected as the lectotype by Wesener (2014: 588), who placed the name in synonymy with the widespread tropical tramp *Rhinotus purpureus* (Pocock, 1894).

A junior synonym of *Rhinotus purpureus* (Pocock, 1894)

metazonalis Saussure & Zehntner, 1902: 224, pl. 15, fig. 17 [*Spirostreptus*].

Madagascar. Col de Sakavalaba (Muséum de Paris, Ch. Alluaud). One ♂.

No specimens found in the MHNG. According to Krabbe (1982) the holotype is in the MNHN, but it is not listed in their online database.

Sechelleptus metazonalis (Saussure & Zehntner, 1902)

micromelas Saussure & Zehntner, 1897: pl. 9, fig. 29 [*Spirostreptus*].

Illustration without description.

Saussure & Zehntner (1902: 218-220) gave a description of the ♂ and the locality information “Madagascar. Sikora 2 ♂ (Musée de Genève)”. The MHNG collection contains two broken specimens in alcohol under the name *Spirostreptus micromelas*. There is also a vial containing a number of fragments including the front of a head, a gnathochilarium and a single gonopod. Both identification labels in the jar have “Madagascar” and one has “Sikora” written on it, indicating that the specimens are syntypes.

Spirostreptus micromelas Saussure & Zehntner, 1897

moramangae Saussure & Zehntner, 1897: pl. 9, fig. 25 [*Alloporus*].

Illustration without description.

Saussure & Zehntner (1902: 175-178) gave a description of both sexes and the locality information “Madagascar. Antananarivo, forêt de Moramanga (F. Sikora 3 ♀, 1 ♂: Musée de Genève).” The MHNG collection contains parts of at least three specimens in alcohol under the name *Alloporus moramangae*. There is a vial with dissected parts, including the gonopods, in the jar. The identification labels both have “Madagascar” written on them and the specimens are presumably syntypes.

Sechelleptus moramangae (Saussure & Zehntner, 1897)

musicus Saussure & Zehntner, 1897: pl. 6, fig. 1 [*Sphaeropoeus*].

Illustration without description.

Saussure & Zehntner (1902: 75-77) gave a description, the locality information “Madagascar, récolté par A. Grandidier” and stated that they had seen at least one ♂. The single male specimen at the MNHN (CH038), collected by A. Grandidier and lacking the telopods, was selected as the lectotype (Wesener & Sierwald, 2005b). The MHNG collection contains dissected parts including the telopods glued to a card mount with the labels “Madagascar, Grandidier” and “*Sphaeromimus musicus* S et Z ♂” on the pin and the label “musicus S et Z, org. copul. ♂, organes de stridulation, Madagascar” pinned in the box next to it; these are probably part of the lectotype. *Sphaeromimus musicus* (Saussure & Zehntner, 1897)

nigrita Saussure & Zehntner, 1897: pl. 6, fig. 6 [*Spirostreptus*].

Illustration without description.

Saussure & Zehntner (1902: 210-212), using the orthography *nigritus*, gave a description of both sexes and the locality information “Madagascar. Antananarivo (F. Sikora): plusieurs individus ♀, 1 ♂ (Musée de Genève)”. The MHNG collection contains parts of more than ten specimens in alcohol under the name *Spirostreptus nigrita*. Many of the specimens are broken; four parts, presumably all from the ♂, have been placed in a vial separately from the rest. The identification labels in the jar have only “Madagascar” written on them, but the specimens are presumably syntypes.

Sechelleptus nigritus (Saussure & Zehntner, 1897)

phthisticus Saussure & Zehntner, 1902: 213-214, pl. 15, fig. 16 [*Spirostreptus*].

Madagascar. Fort Dauphin (Muséum de Paris, M. Alluaud). One ♂.

No specimens found in the MHNG. According to Krabbe (1982) the holotype is in the MNHN but it is not listed in their online database.

Spirostreptus phthisticus Saussure & Zehntner, 1902

pictus Saussure & Zehntner, 1897: pl. 8, fig. 20 [*Spirostreptus*].

Illustration without description.

Saussure & Zehntner (1902: 234-236) gave a description of the ♂, stating that they had one specimen, and the locality information “Madagascar. Tananarive, M. Catat (Muséum de Paris).” No specimens found in the MHNG. According to Krabbe (1982) the holotype is in the MNHN, but it is not listed in their online database.

Spirostreptus pictus Saussure & Zehntner, 1897

piliger Saussure & Zehntner, 1897: pl. 5, fig. 19 [*Sphaerotherium*].

Illustration without description.

Saussure & Zehntner (1902: 36-38, pl. 15, fig. 4), using

the orthography *piligerum*, gave a description and the locality information “Madagascar (Muséum de Paris 2 ♂ récoltés par M. Catat. Musée de Genève 2 ♂)”. The MHNG collection contains two pinned specimens and one specimen in alcohol under the name *Sphaerotherium piliger*. Both pinned specimens have identification labels but no data labels, and both have a card mount on the pin with dissected parts glued to it; in one case the head and telopods, in the other parts of the telopods. The jar containing the specimen in alcohol contains identification labels with “Madagascar” written on them. These are presumably all part of the type series. The only male specimen in the MNHN (MY2973/CB040) was referred to as the holotype by Wesener & Wägele (2008: 57) and was designated as lectotype by Wesener (2016: 84).

Zoosphaerium piligerum (Saussure & Zehntner, 1897)

platylabum Saussure & Zehntner, 1897: pl. 5, fig. 9, pl. 15, fig. 5 [*Sphaerotherium*].

Illustration without description.

Saussure & Zehntner (1902: 54-55) gave a description of the ♂ and the locality information “Madagascar. Tananarive (Muséum de Paris, M. Catat).” The MHNG collection contains a pair of telopods in alcohol under the name *Sphaerotherium platylabum*. A label in the vial containing the parts reads “S. platylabum S. et Z., org. copul.” It seems very likely that this is part of the specimen in the MNHN (CB041/ MY2974) referred to as the holotype by Wesener & Wägele (2008: 50), who noted that the anterior telopods were missing.

Zoosphaerium platylabum (Saussure & Zehntner, 1897)

praslina Saussure & Zehntner, 1897: pl. 10, fig. 37 [*Spirobolus*].

Illustration without description.

Saussure & Zehntner (1902: 124-126), using the orthography *S. (Spiromanes) praslinus*, gave a description, the locality information “Iles Seychelles - Port Praslin, récoltés par M Alluaud (Muséum de Paris)” and stated that they had seen two ♂ and two ♀. No specimens found in the MHNG. The MNHN online database indicates three specimens (MY9480) which are presumably syntypes although not explicitly stated to be. As the only available male type specimen is immature, Mauriès (1980) compared it to a juvenile *Spirostrophus naresi*, a synonym of the widespread tramp *Leptogoniulus sorornus* (Butler, 1876) and found that they are allospecific.

Spirobolus praslinus Saussure & Zehntner, 1897

priapus Saussure & Zehntner, 1897 pl. 4, fig. 5 [*Sphaerotherium*].

Illustration without description.

Saussure & Zehntner (1902: 61-63) gave a description of both sexes but no indication of the type locality or collector. No specimens found in the MHNG. The single ♀ specimen at the MNHN (CB042/MY2975) was

designated as lectotype by Wesener & Wägele (2008: 30).

Zoosphaerium priapus (Saussure & Zehntner, 1897)

prozonalis Saussure & Zehntner, 1902: 231 [*Spirostreptus*].

Madagascar (Musée de Genève). One ♀.

The MHNG collection contains one ♀ specimen in alcohol under the name *Spirostreptus prozonalis*. The jar contains a data label “Ouest-Madagascar, M Voeltzkow.” This specimen is presumably the holotype. The generic placement of this species is uncertain.

“*Spirostreptus*” *prozonalis* Saussure & Zehntner, 1902

pygidiale Saussure & Zehntner, 1897: pl. 5, fig. 8, pl. 14, fig. 22 [*Sphaerotherium*].

Illustration without description.

Saussure & Zehntner (1902: 32-33) gave a description, the locality information “Madagascar. Fianarantsoa (A. Grandidier, plusieurs individus de la partie orientale). Tananarive (Muséum de Paris, M. Catat). Ile Maurice (Robillard, musée de Genève)” and indicated that they had seen many specimens. The MHNG collection contains 12 pinned specimens under the name *Sphaerotherium pygidiale*. There are four specimens labelled “Ile Maurice Robillard”, and four pinned specimens without locality labels on the pins but with “Madagascar (doubles Grandid.)” written on the species name label in the box. Two card mounts on separate pins with dissected parts glued to them are placed with these specimens, each with an identification label; one is correctly labelled as the second pair of legs of a ♀, showing the vulvas, the other is of the same part but incorrectly labelled as ♂. These specimens are clearly part of the type series. There are four more specimens, one of which has the label “Madagascar, Robillard”, which have been identified (although only two have identification labels) as a ♂ variety, presumably the one mentioned in the description of 1902. These specimens should not be regarded as syntypes. There are also two specimens in alcohol under the name *Sphaerotherium pygidiale*, accompanied by a vial containing five pairs of telopods, some broken. The identification labels in the jar have “Madagascar” written on them and the specimens are presumably part of the type series. The MNHN online database lists five syntypes in three lots (MY2976, MY2977 and MY2978) in their collection, of which one ♂ (MNHN CB043) was designated as the lectotype by Wesener & Wägele (2008: 10).

A junior synonym of *Zoosphaerium neptunus* (Butler, 1872)

radamae Saussure & Zehntner, 1897: pl. 9, fig. 32 [*Spirostreptus*].

Illustration without description.

Saussure & Zehntner (1902: 269-272) gave a description of both sexes and the locality information “Madagascar,

Antananarivo, Ankarata (altitude 2,000 pieds) [F. Sikora] (Musée de Genève)." The MHNG collection contains body parts of at least ten specimens in alcohol under the name *Spirostreptus radamae*. The specimens are in one tube, and a separate vial contains gonopods and a gnathochilarium labelled as ♂ and a gnathochilarium labelled as ♀, the two sexes being separated by a cotton wool plug. The identification labels have only "Madagascar" written on them but these specimens are presumably syntypes.

Charactopygus radamae (Saussure & Zehntner, 1897)

rubripes Saussure & Zehntner, 1897: pl. 11, fig. 48 [*Spirobolus*].

Illustration without description.

Saussure & Zehntner (1902: 154-155; pl. 13, fig. 6) gave a description of both sexes and the locality information "Madagascar. Forêts d'Andrangoloaka (Fr. Sikora). Plusieurs individus adultes ♂ et ♀." The MHNG collection contains six specimens in alcohol under the name *Spirobolus rubripes*. The specimens are in one tube, with a second vial containing a partially dissected head and a pair of gonopods. Two identification labels in the jar have "Madagascar (Sikora)" written on them, indicating that they are part of the type series. Wesener *et al.* (2009b: 40) designated a ♂ specimen in MNHN as the lectotype and one ♂ and two ♀ as paralectotypes (MY9723).

Zehntnerobolus rubripes (Saussure & Zehntner, 1897)

sakalava Saussure & Zehntner, 1897: pl. 5, fig. 22 [*Polydesmus*].

Illustration without description.

Saussure & Zehntner (1901: 437; figs 8-10) placed the species in the subgenus *Polydesmus* (*Pterodesmus*), gave a cursory description and the locality information "Nossibé". Saussure & Zehntner (1902: 93, pl. 14, fig. 20) placed the species in the subgenus *Polydesmus* (*Tubercularium*), gave a description of the ♂ and the locality information "Ile de Nosy Bé (Voeltzkow), 1 ♂. Madagascar (Grandidier), 1 ♀ mutilée". The MHNG collection contains one ♀ in alcohol under the name *Phymatodesmus sakalava*. The specimen is broken and the identification label in the vial in which it is contained has "♀ Madagascar (Sikora)" written on it. This specimen is probably not a syntype, but the species is not listed in the online databases of the SMF or the MNHN and a *lapsus calami* cannot be ruled out.

Eutubercularium sakalava (Saussure & Zehntner, 1897)

sakalava Saussure & Zehntner, 1897: pl. 11, fig. 46 [*Spirobolus*].

Illustration without description.

Saussure & Zehntner (1902: 138-140; pl. 13, fig. 1) gave a description of the ♀ and a juvenile ♂, the latter as a variation which means that it should not be considered a syntype. They also gave the locality information "Madagascar. Forêt de Moyamanga (F. Sikora)." The

MHNG collection contains two specimens in alcohol under the name *Spirobolus sakalava*. The ♀ specimen is loose in the jar, the ♂ is in a vial. The identification labels have only "Madagascar" written on them, but there is little doubt that these specimens are part of the type series, and there is a label reading "TYPE" in the jar. Wesener *et al.* (2009a: 38) designated the ♀ specimen in the MNHN (MY6573) as lectotype.

Aphistogoniulus sakalava (Saussure & Zehntner, 1897)

sakalava Saussure & Zehntner, 1897: pl. 9, fig. 28 [*Spirostreptus*].

Illustration without description.

Saussure & Zehntner (1901: 456-457, figs 50-52) gave a description of both sexes and the locality information "Madagascar occidentalis (♀ ♂ a Voeltzkow lecti)." No specimens found in the MHNG. According to Krabbe (1982) the type material is in the SMF, but it is not listed in their online database.

Charactopygus sakalava (Saussure & Zehntner, 1897)

sansibaricum Saussure & Zehntner, 1901: 437-438, fig. 11 [*Strongylosoma*].

Zanzibar, Kokotoni, leg. Voeltzkow. Two ♂.

The MHNG contains one specimen in alcohol under the name *Strongylosoma sansibarica*. The specimen is in a vial, and there is also a micro vial containing two gonopods. The identification labels in the jar have "Zanzibar Dr Voeltzkow" written on them, indicating that the specimen is a syntype. An undated typed label states that Hoffman examined the specimen, regarding it as a type but was uncertain of the generic placement. The other syntype is presumably in the SMF but it is not listed in their online database.

Strongylosoma sansibaricum Saussure & Zehntner, 1902

scabricollis Saussure & Zehntner, 1897: pl. 8, fig. 23 [*Spirostreptus*].

Illustration without description.

Saussure & Zehntner (1902: 199-200) gave a description of both sexes and the locality information "Madagascar - M. Catat et M. Lantz (Muséum de Paris)". No specimens found in the MHNG. According to Krabbe (1982) the type material is in the MNHN, but it is not listed in their online database.

Sechelleptus scabricollis (Saussure & Zehntner, 1897)

sculptus Saussure & Zehntner, 1897: pl. 7, fig. 10 [*Spirostreptus*].

Illustration without description.

Saussure & Zehntner (1902: 201-204) gave a description of the ♂ and the locality information "Madagascar. 1 ♂ récolté par M. Lantz (Muséum de Paris)". No specimens found in the MHNG. According to Krabbe (1982) there are type specimens in the MNHN and the NHMW. The species is not listed in the MNHN online database, or in Enghoff (2003).

Spirostreptus sculptus Saussure & Zehntner, 1897

seychellarum Saussure & Zehntner, 1897: pl. 8, fig. 21, pl. 10, fig. 36 [*Spirobolus*].

Illustration without description.

Saussure & Zehntner (1902: 122-124) gave a description, the locality information “Iles Seychelles, récoltés M. Lantz (Muséum de Paris)” and stated that they had seen three ♂ and one ♀. The generic placement was given as *Spirostreptus* in plate 8, *Spirobolus* in plate 10 and *Spiromanes* (*Spiromanes*) in the description. No specimens found in the MHNG. The MNHN online database lists three specimens (MY3516) which are presumably syntypes although not explicitly stated to be. *Spiromanes seychellarum* (Saussure & Zehntner, 1897)

sikorae Saussure & Zehntner, 1897: pl. 10, fig. 35 [*Spirobolus*].

Illustration without description.

Saussure & Zehntner (1902: 136-137) gave a description of the ♀ and the locality information “Madagascar. Récoltées par F. Sikora, 2 ♀ (Musée de Genève).” The MHNG collection contains two specimens in alcohol under the name *Spirobolus sicoranus*. They are in separate tubes, and accompanied by a vial containing a gnathochilarium. The identification labels in the jar have “Madagascar” written on them. There is also a label reading “TYPE” and a 2012 TW identification label. A label in one of the tubes indicated that it was intended to designate a lectotype, but this designation has not been published. The new generic placement follows TW’s 2012 determination of the specimens.

Hylekobolus sikorae (Saussure & Zehntner, 1897) **comb. nov.**

spinipes Saussure & Zehntner, 1897: pl. 9, fig. 30 [*Spirostreptus*].

Illustration without description.

Saussure & Zehntner (1902: 204-205) gave a description of the ♀ and the locality information “Madagascar. M. Catat (Muséum de Paris).” No specimens found in the MHNG. According to Krabbe (1982) the type material is in the MNHN, but it is not listed in their online database. Considered a nomen dubium by Krabbe (1982). The generic placement is uncertain.

“*Spirostreptus*” *spinipes* Saussure & Zehntner, 1897

stridulator Saussure & Zehntner, 1902: 66-67, pl. 15, fig. 6 [*Sphaerotherium*].

Madagascar. Col de Sakavalana, leg. Alluaud (Muséum de Paris). One ♂.

No specimens found in the MHNG. The MNHN has a single ♂ (MY2981/CB045) identified as the holotype by Wesener & Wägele (2008: 63).

A junior synonym of *Zoosphaerium blandum* (Saussure & Zehntner, 1902)

sulcicollis Saussure & Zehntner, 1897: pl. 2, fig. 8, pl. 7, fig. 18 [*Spirostreptus*].

Illustration without description.

Saussure & Zehntner (1902: 196-199) gave a description of both sexes and the locality information “Madagascar ♂♀ (Alfred Grandidier) – Petit individu (Sikora).” No specimens found in the MHNG. According to Krabbe (1982) there is type material in the MNHN, although this is not listed in their online database.

Sechelleptus sulcicollis (Saussure & Zehntner, 1897)

tricolor Saussure & Zehntner, 1902: 272-274 [*Spirostreptus*].

Madagascar, leg. Catat (Muséum de Paris). One ♀.

No specimens found in the MHNG. According to Krabbe (1982) the holotype is in the MNHN although it is not listed in their online database. The generic placement is uncertain.

?*Charactopygus tricolor* (Saussure & Zehntner, 1902)

univirgatus Saussure & Zehntner, 1897: pl. 11, fig. 47 [*Spirobolus*].

Illustration without description.

Saussure & Zehntner (1901: 444-445; figs 16-19, 56-58) placed this species in the genus *Spiromimus*. They gave a description of both sexes and the locality information “Madagascar, 1 ♀ adulta. Insula Nossibé, ♂ Dr. Voeltzkow legit.” No specimens found in the MHNG or MNHN. The syntypes are presumably in the SMF, but they are not listed in their online database.

Spiromimus univirgatus (Saussure & Zehntner, 1897)

vagabundus Saussure & Zehntner, 1897: pl. 7, fig. 7, pl. 8, fig. 22 [*Spirostreptus*].

Illustration without description.

Saussure & Zehntner (1902: 179-181) placed the species in the genus *Thyropygus*. They gave a description of both sexes and the locality information “Madagascar (Muséum de Paris), ♀ ♂ jeunes. Sumatra, Lahat (Musée de Genève) 2 ♀.” The MHNG collection contains one specimen in alcohol under the name *Thyropygus vagabundus*. There is a vial containing the gnathochilarium in the jar. The identification labels in the jar have “♀ Sumatra” written on them, indicating that the specimen is a syntype. The MNHN presumably has other syntypes but these are not listed in their online database. According to Enghoff (2003) the Madagascar provenance of *T. vagabundus* is probably an error.

Thyropygus vagabundus (Saussure & Zehntner, 1897)

vermiculus Saussure & Zehntner, 1897: pl. 9, fig. 26 [*Spirostreptus*].

Illustration without description.

Saussure & Zehntner (1901: 457-458, figs 53-55) gave a description of both sexes and the locality information “Madagascar occidentalis. Individua plurima a Voeltzkow lecta.” The MHNG collection contains parts of at least three specimens in alcohol under the name *Spirostreptus vermiculus*. The specimens are in a tube

and there is a smaller vial containing a pair of gonopods and two gnathochilaria. One of the identification labels in the jar has "Madagascar occid." written on it, indicating that these specimens are syntypes.

Emmekius vermiculus (Saussure & Zehntner, 1897)

versicolor Saussure & Zehntner, 1897: pl. 7, figs 15-16, pl. 8, fig. 19 [*Spirostreptus*].

Illustration without description.

Saussure & Zehntner (1902: 236-239) gave a description of both sexes and the locality information "Madagascar. ♀ ♂ jeunes récoltés par M. Catat (Muséum de Paris): plusieurs ♀ et un jeune ♂ récoltés par le Dr Keller (Musée de Genève)." The MHNG contains one ♀ specimen in alcohol under the name *Spirostreptus versicolor*. The jar also contains a vial containing the gnathochilarium. The identification labels in the jar have "Madagascar" written on them, and the specimen is presumably a syntype. The whereabouts of the other specimens collected by Keller is unknown. According to Krabbe (1982) there is type material in the MNHN, but this is not listed in their online database.

Spirostreptus versicolor Saussure & Zehntner, 1897

voeltzkowi Saussure & Zehntner, 1901: 445-446, figs 20-26 [*Spirominus*].

Insulae Nossibé et Satakia (Voeltzkow legit). Unspecified number of ♂ and ♀.

Saussure & Zehntner (1902: 164-166, pl. 13, fig. 5) gave the same information about the type series, but placed the species in the genus *Spirobolus* (*Spirominus*). The MHNG collection contains six specimens in alcohol under the name *Spirobolus voeltzkowi*. Four specimens are placed in one tube with a vial containing gonopods and an identification label with "Satakia island, Voeltzkow" written on it. One specimen in its own tube has an identification label with "Satakia island Voeltzkow" written on it. One specimen in its own tube has an identification label with "Nossibé Voeltzkow" written on it, the head and several attached segments, and the gonopods are in a separate vial in the tube. These are all part of the type series. Wesener & Enghoff (2009: 84) designated the ♂ from Nossibé as the lectotype and an immature specimen in the MNHN as paralectotype (MY9804).

Spirominus voeltzkowi Saussure & Zehntner, 1901

voeltzkowianum Saussure & Zehntner, 1897: pl. 5, fig. 21 [*Sphaerotherium*].

Illustration without description.

Saussure & Zehntner (1901: 435-436; figs 6-7 and 36) gave a description of both sexes and the locality information "Madagascar. Plusieurs individus de Nosy Bé, récoltés par le docteur Voeltzkow." The same information is given in Saussure & Zehntner (1902: 52-53, pl. 14, fig. 8, pl. 15, fig. 3). The MHNG collection contains two pinned specimens and six specimens in alcohol (accompanied by a vial containing a broken

pair of telopods) under the name *Sphaerotherium voeltzkowianum*. One of the pinned specimens has the labels "VOELTZKOW", "WEST MADAGASC." and an identification label, and is clearly part of the type series. There is a card mount with the second pair of legs showing the vulvas on the pin. The other is a smaller specimen and the identification label has a question mark on it; this specimen cannot be considered a type. One of the identification labels in the jar has "Madagascar, Dr Voeltzkow" written on it, indicating that these specimens are part of the type series. The one male specimen in the MNHN was designated as lectotype (MNHN CB046) and the two females as paralectotypes by Wesener & Wägele (2008: 43). The rest of the type series is presumably in the SMF but the species is not listed in their online database. The MHNG collection also has a much more recently collected and identified specimen in alcohol under the name *Zoosphaerium voeltzkowianum* which is obviously not part of the type series.

Zoosphaerium voeltzkowianum (Saussure & Zehntner, 1897)

xanthopus Saussure & Zehntner, 1901: 450-451 [*Spirostreptus*].

Madagascar occidentalis leg. Voeltzkow. Unspecified number of ♀.

No specimens found in the MHNG. According to Krabbe (1982) the type material is in the MNHN, but it is not listed in their online database. Considered a nomen dubium by Krabbe (1982). The generic placement is uncertain.

"*Spirostreptus*" *xanthopus* Saussure & Zehntner, 1901

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***Hemigrammus tridens* Eigenmann (Characiformes, Characidae): first records of a small tetra from the Paraná River basin**

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Abstract: *Hemigrammus tridens* is a small characid described by Eigenmann (in Eigenmann & Ogle, 1907) from Paraguay River, in the country Paraguay. The species has a conspicuous trident-shaped caudal spot, few perforated lateral line scales, scales on the caudal fin, and two pentacuspitate teeth in the outer series of the premaxilla. *Hemigrammus tridens* is found in the Paraná River basin of both, Argentina and Paraguay. The records from Argentina are the first for this species in the country. Comments on the type series are added.

Keywords: *Hemigrammus tridens* - Paraná River basin - Argentina - Paraguay - complementary description.

INTRODUCTION

The basin of the Río de la Plata comprises three large rivers: Paraná, Paraguay, and Uruguay. There are several tetras, e.g., *Hemigrammus ulreyi* (Boulenger, 1891) or *Hyphessobrycon elachys* Weitzman, 1985, which live in environments of Paraguay and Paraná Rivers. *Hemigrammus tridens* is a small characid described by Eigenmann (in Eigenmann & Ogle, 1907) based on two specimens from the arroyo Pypucú which is a tributary of the Río Apa (Eigenmann & Kennedy, 1903), Paraguay River basin, in the country Paraguay. Géry (1977) divided the genus *Hemigrammus* in several artificial groups; one of them is the *Hemigrammus-tridens*-group, based on the presence of a caudal spot, usually a longitudinal band or line along body and the absence of a humeral spot. Britski *et al.* (1999) mentioned its presence among the ichthyofauna of the Pantanal, Paraguay River basin (Mato Grosso, Brazil), and it was cited in several papers, usually, associated to descriptions of species: Uj & Géry (1989), Zarske & Géry (2002, as *Hyphessobrycon tridens*), Bertaco & Carvalho (2005), and Carvalho *et al.* (2010). For other collecting localities see Ota (2010) who included *H. tridens* in her thesis about the species of the genus *Hemigrammus* Gill, 1858 in the Paraguay River basin. The objective of this short contribution is to record this small tetra found at environments of the Paraná River, in the Provinces of Corrientes and Chaco, Argentina, and to report its presence in the Paraná River basin of the country Paraguay. The records from Argentina are the first for this species in the country.

MATERIAL AND METHODS

Specimens were fixed in formaldehyde and subsequently transferred to ethanol 70%. Measurements were taken following Fink & Weitzmann (1974), and are indicated in Table 1. Counts indicate the value followed by the number of specimens between brackets. Institutional abbreviations follow Sabaj-Pérez (2016).

Material examined

Paraguay River basin:

CAS 58609, photograph of holotype, *Hemigrammus tridens* Eigenmann, 1907.

MHNG 2544.071, 3 specimens, 15.5-18.2 mm SL, Paraguay, Concepción, Riacho El Postillón, 6 km from Puerto Max, coll.: F. Baud, C. Dlouhy, V. Mahnert, J.-L. Perret, C. Vaucher, B. Jacquet, and A. Colman. October 20, 1979.

Paraná River basin:

MHNG 2179.022, 1 specimen, 19.5 mm SL, Argentina, Chaco, Puerto Tirol, affluent of a lagoon, coll.: A. Pira.

MHNG 2678.025, 5 specimens (3 measured, 1 female, 3 males), 16.5-17.3 mm SL, Argentina, Corrientes, Depto. San Cosme, RN 12, km 1072, 27°22'34"S-58°23'47"W (taken from Google Earth), permanent lake in the premises of Olho-Porá, coll.: S. Koerber and J.O. Fernández Santos, September 23, 1995.

Table 1. Measurements of nine specimens of *Hemigrammus tridens* from the Paraná River basin in Argentina and Paraguay. Güyraugua N=5. San Cosme N=3. Puerto Tirol N=1.

<i>Hemigrammus tridens</i>	Paraguay		Argentina		Argentina Puerto Tirol
	Güyraugua		San Cosme		
	min	max	min	max	
SL	15.00	16.90	16.50	17.30	19.50
Percentage in SL					
predorsal length	1.67	1.84	2.2	2.4	1.86
prepelvic length	1.75	2.01	1.76	1.84	1.88
preanal length	1.48	1.56	1.48	1.59	1.47
maximum body depth	2.78	2.95	2.89	3.00	3.07
head length	3.16	3.25	3.05	3.11	3.36
anal-fin base	3.78	3.9	4.12	4.2	3.82
pectoral length	5.0	3.96	4.17	4.71	4.02
ventral length	3.95	4.84	4.24	4.71	4.43
pelvic fin/anal fin length*	2.8	3.05	2.73	2.84	2.63
anal fin/caudal rays length**	2.56	2.67	2.63	2.74	2.56
Percentage in head length					
snout	3.69	4.08	3.7	3.92	3.6
eye	2.00	2.22	2.29	2.54	1.98
interorbital distance	3.06	3.69	2.94	3.17	3.05
postorbital distance	2.04	2.4	2.1	2.43	2.14

*length between pelvic-fin origin and anal-fin origin; **length between anal-fin origin and middle caudal-fin rays.

CI-FML 7107 (ex MHNG 2742.079), 8 specimens, 15.0-16.9 mm SL, Paraguay, Caaguazú, small tributary of Río Güyraugua, Paraná River basin, South of the route between Asunción and Ciudad del Este, coll.: S. Fisch-Muller, C. Dlouhy and V. Mahnert, July 11, 1990.

MLP 10917 (ex MHNG 2742.079), 2 specimens, 16.4-17.2 mm SL, all collecting data same as of previous.

MHNG 2494.019, 2 specimens, 17.4-18.4 mm SL, Paraguay, Itapúa, arroyo Pirayu-í, coll.: C. Weber and C. Dlouhy, October 10, 1986.

RESULTS

Hemigrammus tridens (Figs 1-2) has a conspicuous caudal-fin spot as a “jet-black band” across the end of the caudal peduncle and caudal fin. It extends forward, forming a blunt median point and backward along edge of caudal-fin rays also, especially marked in the base of middle caudal-fin rays. Thin lateral band along body. Humeral spot absent or present as a very faint spot of scattered chromatophores.

Origin of dorsal fin nearer caudal fin than eye; dorsal fin ii,9 rays (9). Pectoral fin falling short anal-fin origin or surpassing it in males, pectoral fin with i,10(3),11(6) rays. Pelvic fin with i,7 rays, surpassing anal fin origin; pelvic-fin origin in a vertical through second or third scale anterior to dorsal-fin origin; pelvic fin with hooks in all branched rays. Anal fin short with iii-iv,15(2),16(3),17(4) rays; its origin in a vertical through second scale posterior to last dorsal-fin ray insertion; anal fin of males with anterior lobe very well developed, formed by six or seven branched rays. Hooks developed from last unbranched anal-fin ray to middle anal-fin length in most specimens (Fig. 3) although one specimen with hooks until last rays. Anal-fin hooks large, located one pair per segment, up to 12 in a ray, in both branches, and decreasing in number backward. Snout short; eye larger than snout; mouth terminal, at horizontal through upper half of eye. Maxilla long, surpassing anterior margin of eye. Two maxillary teeth, pentacuspitate. Premaxilla with an inner series of five teeth and an outer series formed by two teeth, all of them pentacuspitate (Fig. 4). Dentary with three or four large teeth followed by three to five small teeth. Three or four first teeth pentacuspitate,

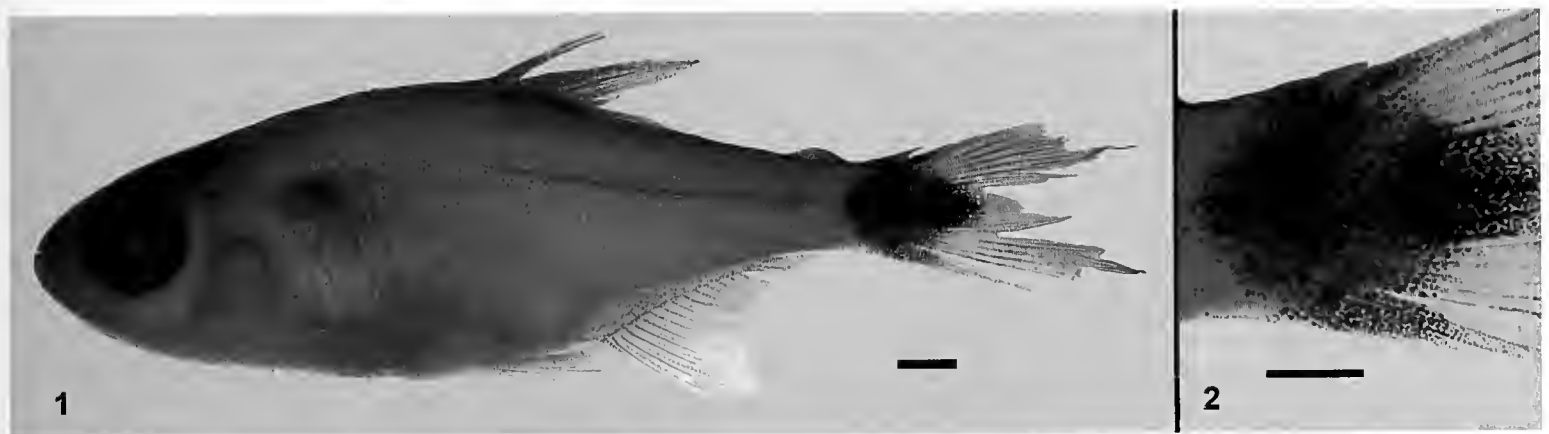
remaining teeth tricuspidate or conic. Number of lateral line scales: 30(5) or 31(4); perforated scales of lateral line: 3(1),4(3),5(2),6(3); transverse scales: 5/3-3.5(3) or 5/3.5(6).

DISCUSSION

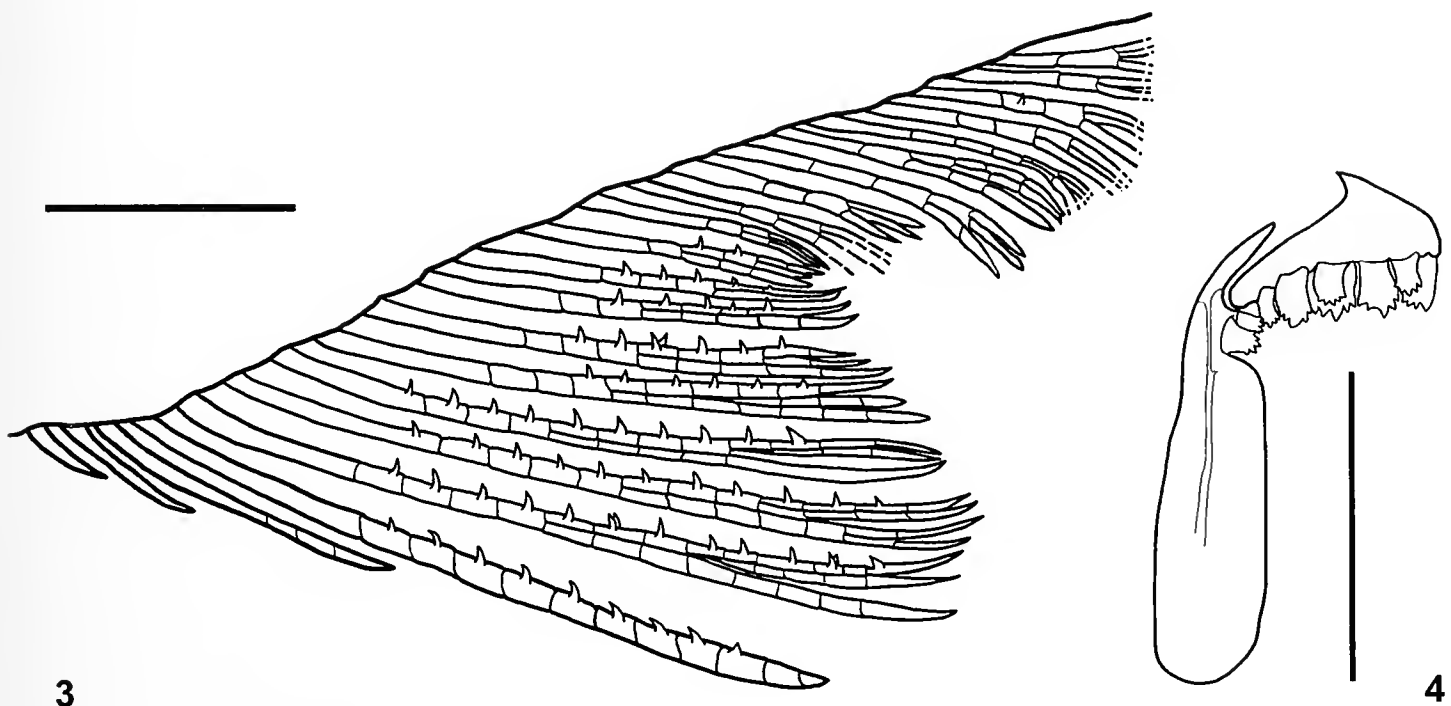
Eigenmann & Ogle (1907) commented that species of *Hemigrammus* Gill, 1858 differ from *Astyanax* Baird & Girard, 1854, by the incomplete lateral line. Nonetheless, the diagnosis of the genus *Hemigrammus* following Eigenmann (1918) is based on the presence of an incomplete lateral line, caudal fin scaled, premaxillary teeth in two rows, and maxillary teeth lacking or reduced in number, restricted to the upper portion of the bone, a definition still in usage. Ota (2010) considered that

the humeral spot of *H. tridens* – if present – is only a faded concentration of chromatophores in the study of the genus *Hemigrammus* from Paraguay Basin. The genus, considered today within *Pristellinae* (Géry & Boutière, 1964; Eschmeyer *et al.*, 2016), contains about 60 species. Uj & Géry (1989) discussed the inclusion of *H. tridens* in the genus because they could not find scales in the caudal fin. However, in the material examined, few specimens from the Paraná river basin have scales in the caudal fin. The small scales of the caudal fin fall down easily. Ota (2010) examined a large number of specimens, many of them without caudal-fin scales, considering that those small scales may be lost.

Hemigrammus tridens was so far only known from several localities in the Paraguay River basin. The specimens examined belong to three collecting sites of the Paraná River basin, downstream from its confluence



Figs 1-2. (1) *Hemigrammus tridens*, MHNG 2678.025, 17.3 mm SL, male. (2) Detail of the caudal spot. Scale bars = 1 mm.



Figs 3-4. (3) *Hemigrammus tridens*, MHNG 2678.025, 17.3 mm SL, male, anal fin with hooks. (4) *Hemigrammus tridens*, CI-FML 7107, 17.0 mm SL, female, premaxilla and maxilla. Scale bars = 1 mm.

with the Paraguay River (Fig. 5). Güyraugua river is a tributary of Monday river in the country Paraguay. Puerto Tirol is located on the coast of Paraná River in Argentina. The environment in which *H. tridens* was collected close to San Cosme is a permanent lake, more than 1 m deep, with profuse vegetation and abundant wood on substrate (Fig. 6). In this habitat the following species were found: *Aphyocharax nattereri*, *Hyphessobrycon elachys*, *H. eques*, *H. igneus*, *H. luetkenii*, *Moenkhausia dichroua*, *Serrapinnus calliurus*, *Pyrrhulina australis*, *Apistogramma borellii*, *Cichlasoma dimerus*, and *Laetacara dorsigera* (captured in December 1994 and/or September 1995).

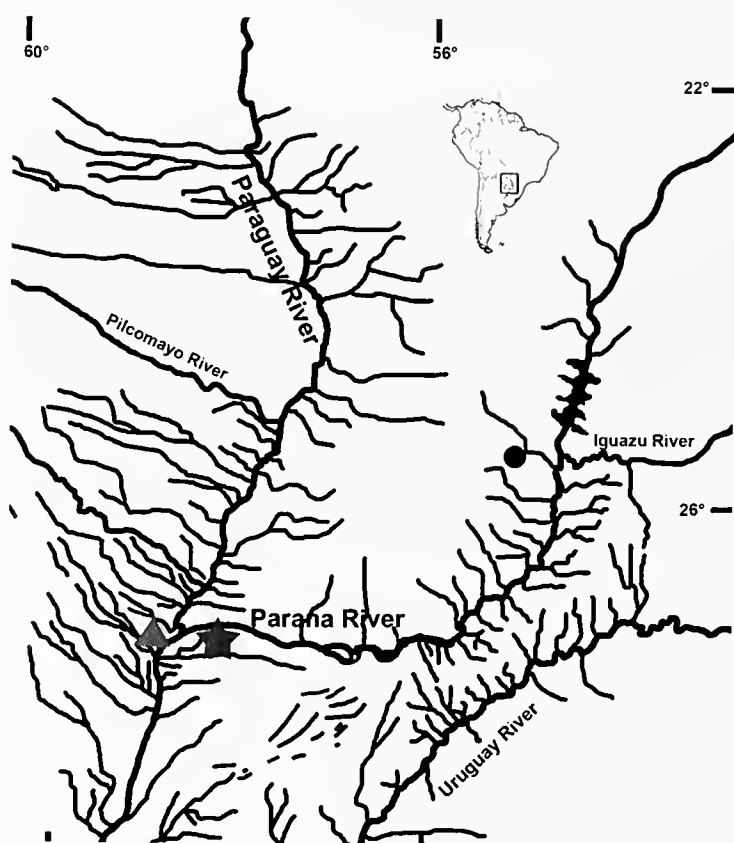


Fig. 5. Map showing the three collecting sites of *Hemigrammus tridens* in the Paraná Basin. Circle: Paraguay (Country), Güyraugua River; star: Argentina, Corrientes, San Cosme; triangle: Argentina, Chaco, Puerto Tirol.

COMMENTS ON THE STATUS OF THE TYPE SPECIMENS

Eigenmann & Ogle (1907) described *Hemigrammus tridens* based on two specimens, designated “Type” and “Cotype”, from the Pypucú stream in Paraguay, being then deposited both at the Indiana University collection (IU 11262). These specimens are today housed at the California Academy of Sciences in the lots CAS 58609 (holotype) and CAS 61474 (paratype). This type status is supported by the article 72.4.6 of the International Code of Zoological Nomenclature (1999). A decade



Fig. 6. Permanent lake close to San Cosme (27°22'34"S-58°23'47"W), RN 12, km 1072, Depto. San Cosme, Corrientes, Argentina.

later, Eigenmann (1918) mentioned a third specimen from the same locality which was not included in the original description. This additional specimen is also still available in San Francisco (CAS 61475) and the CAS online database states that it was initially also from lot IU 11262 with the remark as “collected w/ type series, but non-type” because the article before mentioned expressly excluded other specimens not nominated as types. Eschmeyer *et al.* (2016) list a potential additional paratype specimen from the collection of Zoologisches Museum Berlin as “?ZMB 17146 [from Eigenmann] (1) Corumbá”. This specimen is available in the ZMB-collection. The respective label states “Typus”, probably noted on the label by August Brauer (Peter Bartsch, pers. comm.), director of ZMB from 1906 to 1917. Also, the label provides information about Eigenmann and Anisits as donators, Anisits as collector and 328 as Anisits’ collector’s field number. The ZMB holds yet another specimen (ZMB 17258) from Corumbá with Anisits’ collector’s number 305a. This one is not labeled as type. Eigenmann *et al.* (1907) have seen specimens from the afore mentioned collector’s lots, but they did not identify the specimens as *Hemigrammus tridens*. In this paper, specimens from Anisits’ lot 328 are mentioned as *Hemigrammus ulreyi* from Corumbá and from lot 305, as small individuals similar to *Moenkhausia agassizii*. As both papers were published in 1907, one would expect that Eigenmann had recognized additional specimens of *Hemigrammus tridens* while determining these lots. Anisits spent nearly his whole professional life in Paraguay; around 1907 he moved to Berlin where he passed away in 1911 (Zarske, 2012). One year after his death, a note was published (Anisits, 1912) in which he confirmed that he did not send all material to Eigenmann but retained what he considered duplicates for his own further studies and that he donated those to the ZMB-collection. It is a mandatory condition for types that the author/s of a new species has determined the specimens.

Considering the article 72.4.6 the specimens in the Collection of the ZMB are not type material. Also, article 72.4.1.1 does not apply in this case.

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Authors thank S. Fisch-Muller for the donation of specimens from Paraguay, A. Vanegas-Ríos and S. Gouiric-Cavalli for the photographs of the specimen, the late J.O. Fernández Santos for his expertise in the field, F. Carvalho for several suggestions on the manuscript, P. Bartsch for information about the material in ZMB.

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Trachyuropodid mites (Acari: Uropodina) from South-East Asia: catalog, new key and description of two new species

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Abstract: All trachyuropodid mites described from South-East Asia are presented in a new illustrated key. Two new species of *Bostocktrachys* (*B. surinensis* sp. nov. and *B. thailandica* sp. nov.) from Thailand are described and illustrated. Both new *Bostocktrachys* species differ from the other known species of this genus by the strongly sclerotized lines of the dorsal shield. Four new combinations are proposed: *Trachyuropoda* (*Leonardiella*) *imitans* Berlese, 1905 is transferred to the genus *Arculatastrachys*, *Trachyuropoda cistulata* Hirschmann, 1975 is placed in the genus *Leonardiella*, *Trachyuropoda micherdzinskii* Hirschmann, 1976 and *Trachyuropoda tuberculata* Berlese, 1913 in the genus *Bostocktrachys*.

Keywords: Turtle mites - taxonomy - zoogeography - Oriental region.

INTRODUCTION

The Uropodina family Trachyuropodidae consists of very unusual and unique mites. Species of this family have numerous particular characters, like the internal malae subdivided into several branches with fringed margins, hypostomal setae not situated in a longitudinal row, and the idiosoma strongly sclerotized and usually equipped with numerous elevated structures (grooves, lines, rings, etc.) on the dorsal shield (Kontschán, 2015).

Currently more than 100 trachyuropodid species are known from around the world (Wiśniewski & Hirschmann, 1993). The most intensively studied area is South America from where more than 30 species are known (Kontschán, 2011c; Kontschán & Starý, 2013). South-East Asia is a poorly-studied part of the world from a trachyuropodid point of view; only six species are listed from this region (Wiśniewski, 1993a; Kontschán, 2015).

New investigations of the Uropodina fauna of South-East Asia started in the last few years. Several new species were discovered and described from Thailand, Vietnam and Malaysia (Kontschán, 2008, 2010a, b, c, 2011a, b; Kontschán & Starý, 2011, 2012), but among them was only one trachyuropodid mite (Kontschán, 2015).

MATERIAL AND METHODS

Specimens of the two new species described here were sorted out from the Arachnida collection of the Natural History Museum in Geneva by the first author. They were cleared in lactic acid, investigated on half covered slides with a well, and illustrations were made with the aid of a drawing tube on a Leica 1000 scientific microscope. All specimens are stored in ethanol and deposited in the Muséum d'histoire naturelle de Genève (MHNG).

Abbreviations of morphological structures: h = hypostomal setae, St = sternal setae, V = ventral setae. All measurements and the scales in the figures are given in micrometres (µm).

RESULTS

List of the known South-East Asian trachyuropodid mites

Arculatastrachys imitans (Berlese, 1905) comb. nov.

Trachyuropoda (*Leonardiella*) *imitans* Berlese, 1905: 159, fig. 14. – Wiśniewski & Hirschmann, 1993: 85. – Wiśniewski, 1993a: 278-278. – Wiśniewski, 1993b: 399.

Distribution: Indonesia (Java).

Justification: Judging from the large, kidney-shaped lateral depressions in the dorsal idiosoma which were illustrated by Berlese (1905), we transfer this species from the genus *Trachyuropoda* to the genus *Arculatatrachys*.

***Leonardiella cistulata* (Hirschmann, 1975) comb. nov.**

Trachyuropoda cistulata Hirschmann, 1975: 103-104, fig. 115.
– Wiśniewski & Hirschmann, 1993: 87. – Wiśniewski, 1993a: 276. – Wiśniewski, 1993b: 398.

Distribution: Sri Lanka.

Justification: Due to the triangular shape of the idiosoma and the presence of a ventral depression posterior to coxae IV (see Hirschmann, 1975) we transfer this species from the genus *Trachyuropoda* to *Leonardiella*.

***Trachyibana sarawakiensis* Kontschán, 2015**

Trachyibana sarawakiensis Kontschán, 2015: 273-277, figs 1-18.

Distribution: East Malaysia (Sarawak).

***Bostocktrachys micherdzinskii* (Hirschmann, 1976) comb. nov.**

Trachyuropoda micherdzinskii Hirschmann, 1976: 29-30, fig. 18. – Wiśniewski & Hirschmann, 1993: 86. – Wiśniewski, 1993a: 277. – Wiśniewski, 1993b: 399.

Distribution: Vietnam.

Justification: See the next species.

***Bostocktrachys tuberculata* (Berlese, 1913) comb. nov.**

Trachyuropoda tuberculata Berlese, 1913: 85, fig. 14.
– Hirschmann & Zirngiebl-Nicol, 1969: 131. – Wiśniewski & Hirschmann, 1993: 86. – Wiśniewski, 1993a: 277-278. – Wiśniewski, 1993b: 400.

Distribution: Vietnam and Indonesia (Java).

Justification: Both *B. tuberculata* and *B. micherdzinskii* have a horizontal furrow on the dorsal shield which is a diagnostic character of the genus *Bostocktrachys*, therefore we transfer these species to the genus *Bostocktrachys*.

***Bostocktrachys surinensis* sp. nov.**

Figs 1-14

Holotype: MHNG, sample TL-15/09; female; Thailand, Surin Province & District, mixed evergreen-deciduous

forest near prison, 14°52'36"N, 103°27'24"E, 150 m, 9.VII.2014; leg. P. Schwendinger.

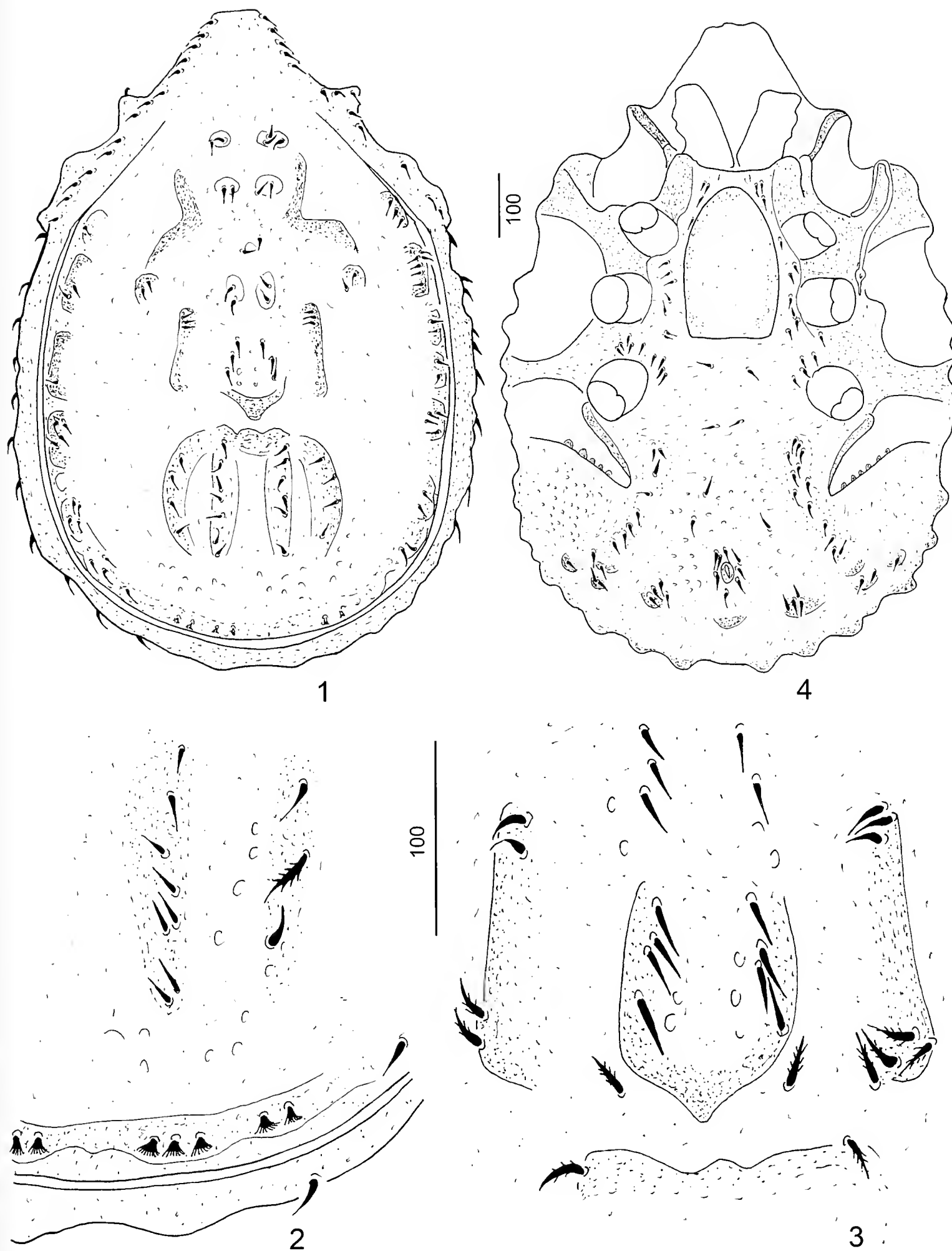
Paratypes: MHNG; two females and two males with same data as for the holotype.

Diagnosis: Distinguished from the other two known *Bostocktrachys* species by smooth and spiniform dorsal setae, except for five pairs of short and apically pilose setae situated close to posterior margin of dorsal shield. Four vertical grooves with a strongly sclerotized horizontal crossbar situated posterior to horizontal furrow. Surface of genital shield of female smooth. Position and shape of strongly sclerotized dorsal grooves and humps unique within the genus *Bostocktrachys*. Only one species in this genus (*B. micherdzinskii*) has short apically serrate caudal setae. Beside the dorsal characters, the most important differences between these two species is the sculptural pattern of the female genital shield, which is smooth in the new species and ornamented with oval pits in *B. micherdzinskii*.

Description of female: Length of idiosoma 1000, width 700. Shape oval, with vertex slightly elongated; posterior margin rounded. Color reddish brown.

Dorsal idiosoma (Fig. 1): Dorsal and marginal shields fused anteriorly. Dorsal shield neutrichous, majority of dorsal setae spiniform (about 21-27 long) some of them pilose, others smooth (Figs 2-3). Ten short (about 8-10 long) and apically pilose setae in four groups (2-3-3-2) situated close to caudal margin of dorsal shield. Surface of dorsal shield bearing numerous strongly sclerotized structures. Numerous short, strongly sclerotized grooves situated close to margins of dorsal shield. One pair of large L-shaped grooves in anterior area of dorsal shield, one pair of C-shaped grooves located near end of L-shaped structures. A deep transversal furrow situated in central area of dorsal shield, anterior to furrow with one pair of long strongly sclerotized grooves and a V-shaped strongly sclerotized structure. Four longitudinal grooves anteriorly connected by a strongly sclerotized transversal crossbar situated posterior to transversal furrow. Surface of dorsal shield with some oval pits. Marginal shield without sculptural pattern; with spiniform setae (about 24-31 in length).

Ventral idiosoma (Fig. 4): Tritosternum with narrow and oval basis; laciniae with two smooth inner and two apically pilose outer branches (Fig. 6). Sternal shield without sculptural pattern and bearing smooth, short (about 16-20 in length) and needle-like setae. Numerous setae visible close to coxae IV. One pair of lyriform fissures situated close to anterior margin of sternal shield. Genital shield scutiform (about 235 long and about 145 wide) its surface smooth (Fig. 5). Ventral shield with oval pits, bearing smooth and needle like seta (about 24-28 long). Numerous setae situated in a horizontal row posterior to coxae IV, some setae placed on three



Figs 1-4. *Bostocktrachys surinensis* sp. nov., female holotype. (1) Dorsal idiosoma. (2) Setae on caudal margin and caudal part of dorsal shield. (3) Area posterior and anterior to transversal dorsal furrow. (4) Ventral idiosoma.

strongly sclerotized humps close to caudal margin. Setae around anal opening similar in shape and length to other ventral setae. Stigmata situated between coxae II and III. Prestigmatic part of peritremes long and hook-shaped, poststigmatic part short (Fig. 4). Pedofossae deep, their surface smooth, only some denticles visible on posterior margins of pedofossae IV.

Gnathosoma (Fig. 7): Corniculi horn-like, internal malae longer than corniculi and divided into four fringed branches. Hypostomal setae h1 short (about 28-30 in length) and smooth, h2-h4 marginally serrate, h2 and h4 short (about 50-55 in length), h3 long (about 93-95 in length), h3 situated close to h2. Deutosternal region smooth. Palpal trochanter with one short and smooth, and one long and marginally serrate seta. Other setae on palp smooth and needle-like, except for one pilose seta on dorsal side of femur; palpal claw bifurcate. Epistome subtriangular and deeply serrate on anterior margin (Fig. 8). Chelicerae with one tooth on movable and fixed digit, fixed digit longer than movable digit, pilus dentilis absent, internal sclerotized node present, one dorsal seta present (Fig. 9).

Legs (Figs 11-14): Leg I 400-410 long, leg II 345-350, leg III 365-375, leg IV 420-430. Legs I-IV each with a pair of claws at tip of ambulacral prolongation; claws of legs I smallest. Most setae on legs needle-like, several robust and serrate setae situated on all legs. Flap-like processes present on femora II-IV and coxa I.

Description of male: Length of idiosoma 960-1000, width 660-700 (n=3). Shape same as in females.

Dorsal idiosoma: Ornamentation and chaetotaxy of dorsal shield as in female.

Ventral idiosoma: Ornamentation and chaetotaxy of ventral shield as in female. Sternal shield without sculptural pattern (Fig. 10). Positions of sternal setae as in Fig. 10. Sternal setae smooth and needle-like (about 15-20 long), one pair of lyriform fissures situated close to first sternal setae. Genital shield rounded (about 53-55 × 62-65 in dimension) and placed between coxae III. Other characters same as in female.

Nymph and larva unknown.

Etymology: The name of the new species refers to the province where the type specimens were collected.

***Bostocktrachys thailandica* sp. nov.**

Figs 15-27

Holotype: MHNG, sample 24-Th-79; female; Thailand, Bangkok, soil sample from base of tree; Berlese-extraction in Geneva; 17.VIII.1979; leg. J. Robert.

Paratypes: MHNG; two females and one male with same data as for holotype.

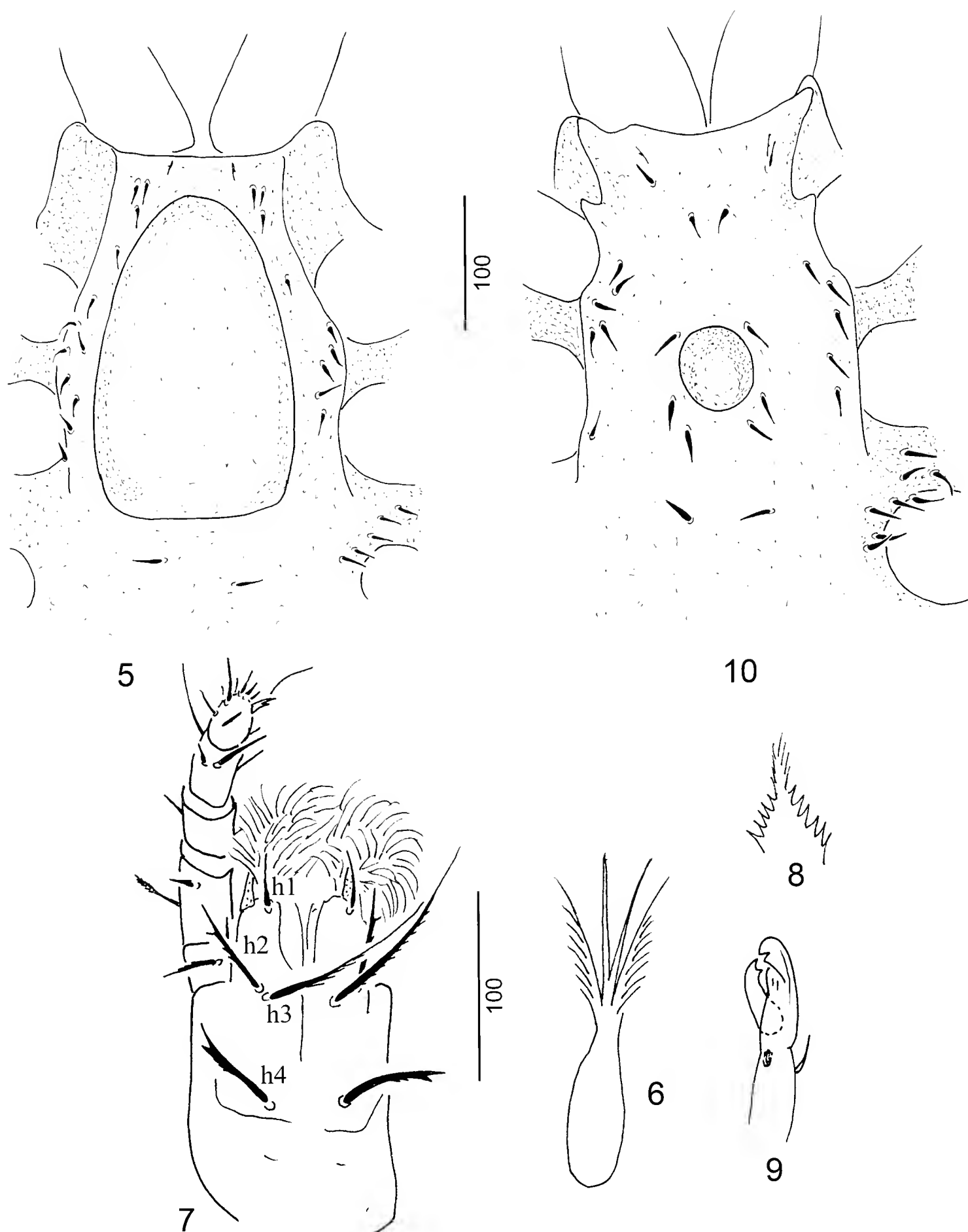
Diagnosis: Distinguished from the other congeneric species by most of dorsal setae smooth and spiniform. Anterior margin of furrow borders wide, elevated area

with strongly sclerotized and V-shaped posterior margin. Anterior parts of elevated area forming one pair of L-shaped, strongly sclerotized structures with deep pits at their corners. Deep horizontal furrow bordered in posterior part with a wide U-shaped sclerotized area. Only *Bostocktrachys tuberculata* has similar strongly sclerotized dorsal structures. In *B. tuberculata* the elevated area posterior to the furrow is rounded and narrower than the elevated area anterior to the furrow, whereas in the new species it is quadrangular and as wide as the elevated area anterior to the furrow. The posterior margin of the elevated area anterior to the transversal furrow also differs: it is straight in *B. tuberculata*, but slightly bent in the new species.

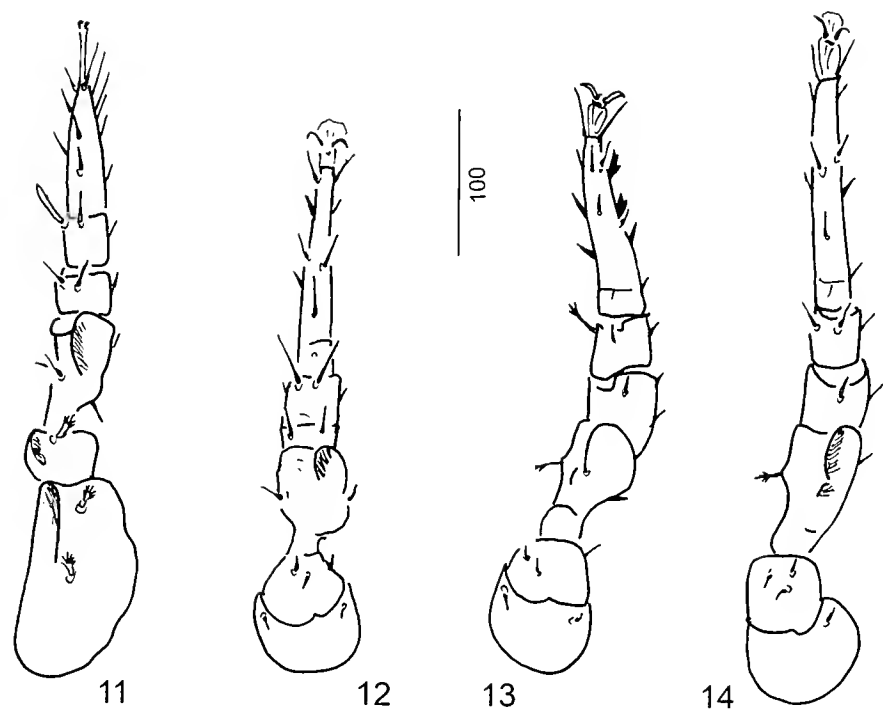
Description of female: Length of idiosoma 1065-1120, width 700-795 (n=3). Shape oval, with vertex slightly elongated, posterior margin rounded. Color reddish brown.

Dorsal idiosoma (Fig. 15): Dorsal and marginal shields fused anteriorly. Dorsal shield neutrichous, majority of dorsal setae spiniform (about 32-44 long), some of them pilose, others smooth. Surface of dorsal shield with oval pits and bearing numerous strongly sclerotized structures. A deep transversal furrow situated in central area of dorsal shield. One pair of strongly sclerotized rings visible at lateral ends of furrow. Anterior margin of furrow borders forming a wide and elevated area with strongly sclerotized and V-shaped posterior margin. Anterior parts of elevated area forming one pair of L-shaped, strongly sclerotized structures with deep pits at their corners. Deep transversal furrow bordered in posterior part by a wide U-shaped sclerotized area bearing pilose setae on margins and smooth setae in central area. Numerous C-shaped humps situated close to lateral and caudal margins of dorsal shield, these humps bearing smooth setae. Marginal shield without sculptural pattern and bearing spiniform setae (about 33-42 long).

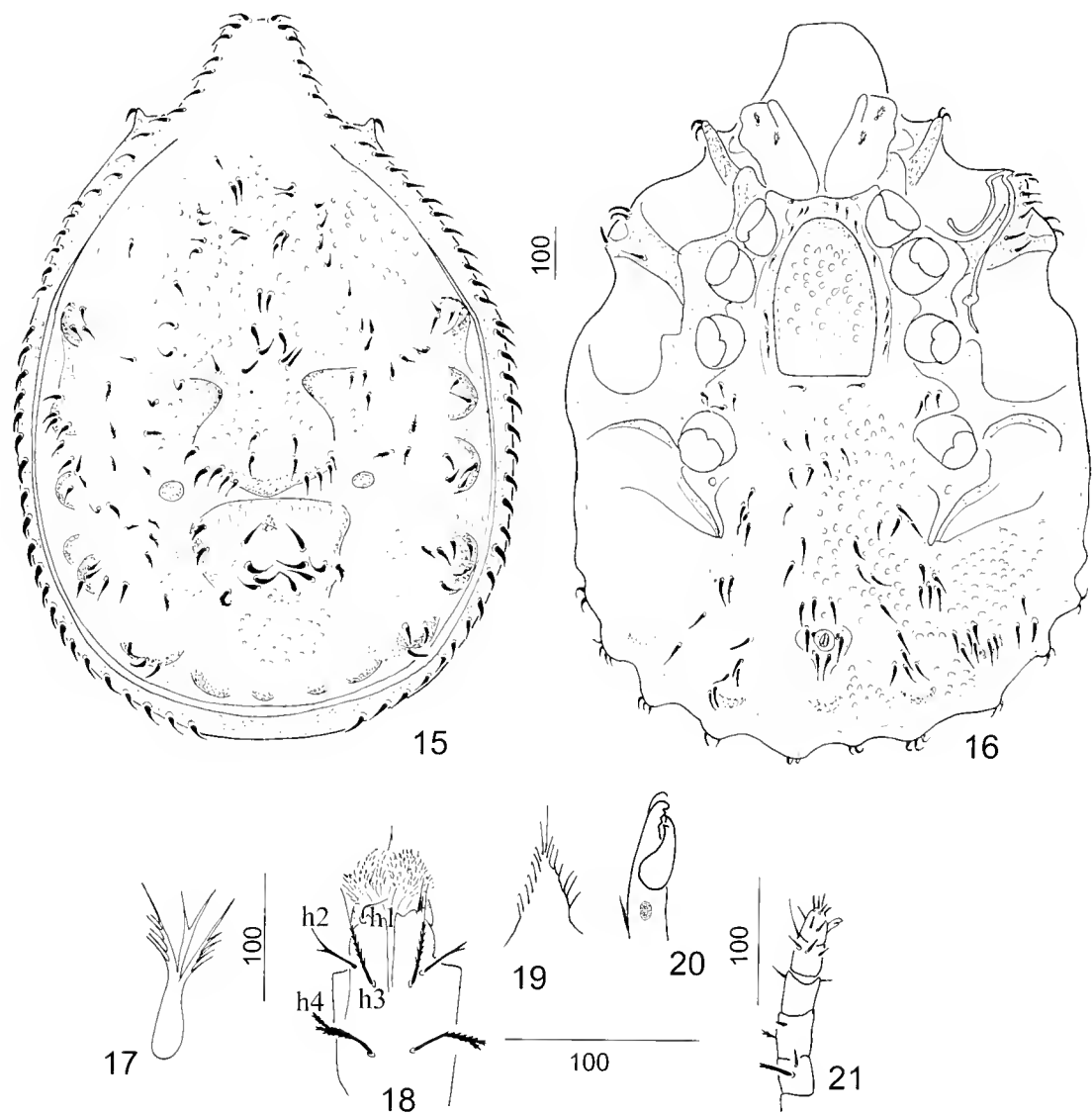
Ventral idiosoma (Fig. 16): Tritosternum with narrow and oval basis; laciniae with two smooth inner and two apically pilose outer branches (Fig. 17). Sternal shield without sculptural pattern. First three pairs of sternal setae serrate, others smooth and needle-like, all sternal setae short (about 18-21 in length). Numerous setae visible close to coxae IV. One pair of lyriform fissures situated close to anterior margin of sternal shield, another pair situated in central area of sternal shield, a third pair at level of posterior margin of coxae III and a fourth pair at level of central area of coxae IV. Genital shield scutiform (about 260-270 long and 170-180 wide), its surface with oval pits (Fig. 22). Ventral shield ornamented with oval pits, bearing smooth and needle-like setae, shape similar to sternal setae but longer (about 30-36). Numerous setae situated in a transversal row posterior to coxae IV; in central section of each row one pair of humps carrying numerous setae. Similar humps with setae situated close to caudal margin of ventral idiosoma. Anal opening



Figs 5-10. *Bostocktrachys surinensis* sp. nov., female holotype (5-9) and male paratype (10). (5, 10) Intercoxal area. (6) Tritosternum. (7) Ventral view of gnathosoma and palp. (8) Epistome. (9) Lateral view of chelicera.



Figs 11-14. *Bostocktrachys surinensis* sp. nov., female holotype. (11) Ventral view of leg I. (12) Ventral view of leg II. (13) Ventral view of leg III. (14) Ventral view of leg IV.



Figs 15-21. *Bostocktrachys thailandica* sp. nov., female holotype. (15) Dorsal idiosoma. (16) Ventral idiosoma. (17) Tritosternum. (18) Ventral view of gnathosoma. (19) Epistome. (20) Lateral view of chelicera. (21) Ventral view of palp.

situated in a drop-shaped area bearing four setae similar in shape and length to other ventral setae plus one pair of lyriform fissures. Stigmata situated between coxae II and III. Prestigmatic part of peritremes long and hook-shaped, poststigmatic part short. Pedofossae deep, their surface smooth.

Gnathosoma (Fig. 18): Corniculi horn-like, internal malae longer than corniculi and divided into four fringed branches. Hypostomal setae h1 short (about 25-27 in length) and smooth, h2 and h4 apically bifurcated, h2 smooth, h3 and h4 marginally serrate, h2 and h4 short (about 45-55), h3 long (about 75-80), h3 situated close to h2. Palpal trochanter with one short and smooth, and one long and serrate ventral seta. Other setae on palp smooth and needle-like, except for one pilose seta on dorsal side of femur (Fig. 21). Epistome subtriangular and strongly serrate on lateral margins (Fig. 19). Chelicerae with one tooth each on movable and fixed digit, fixed digit longer than movable digit, pilus dentilus absent, internal sclerotized node and one dorsal seta present (Fig. 20).

Legs (Figs 23-26): Leg I 460-465 long, leg II 400-410, leg III 420-430, leg IV 460-465. Legs I-IV each with a pair of claws at tip of ambulacral process, claws of legs I smallest. Most setae on legs needle-like, some robust and serrate setae situated on all legs. Flap-like processes on femora II-IV.

Description of male: Length of idiosoma 1120, width 745 (n=1). Shape same as in females.

Dorsal idiosoma: Ornamentation and chaetotaxy of dorsal shield as in female.

Ventral idiosoma: Ornamentation and chaetotaxy of ventral shield as in female. Sternal shield without sculptural pattern (Fig. 27). Sternal setae smooth and needle-like (about 17-20 long), situated close to margins of sternal shield and around genital opening (Fig. 27). Genital shield rounded (about 47×50 in dimension) and situated between coxae III-IV. Other characters as in female.

Nymph and larva unknown.

Etymology: The name of the new species refers to the country where the type specimens were collected.

DISCUSSION

The majority of trachyuropodid mites were collected in association with ants, often from the hole of anthills. This was very often the case in European species (Mašán, 2001), whereas numerous non-European species were found without ants, in moss, soil and leaf litter (Kontschán, 2011c). The fact that the two new *Bostocktrachys* species described here were collected from soil and leaf litter is thus not unusual. These species either live without an association with ants or they were extracted from leaf litter samples which contained very small ant nests.

The trachyuropodid fauna of South-East Asia remains

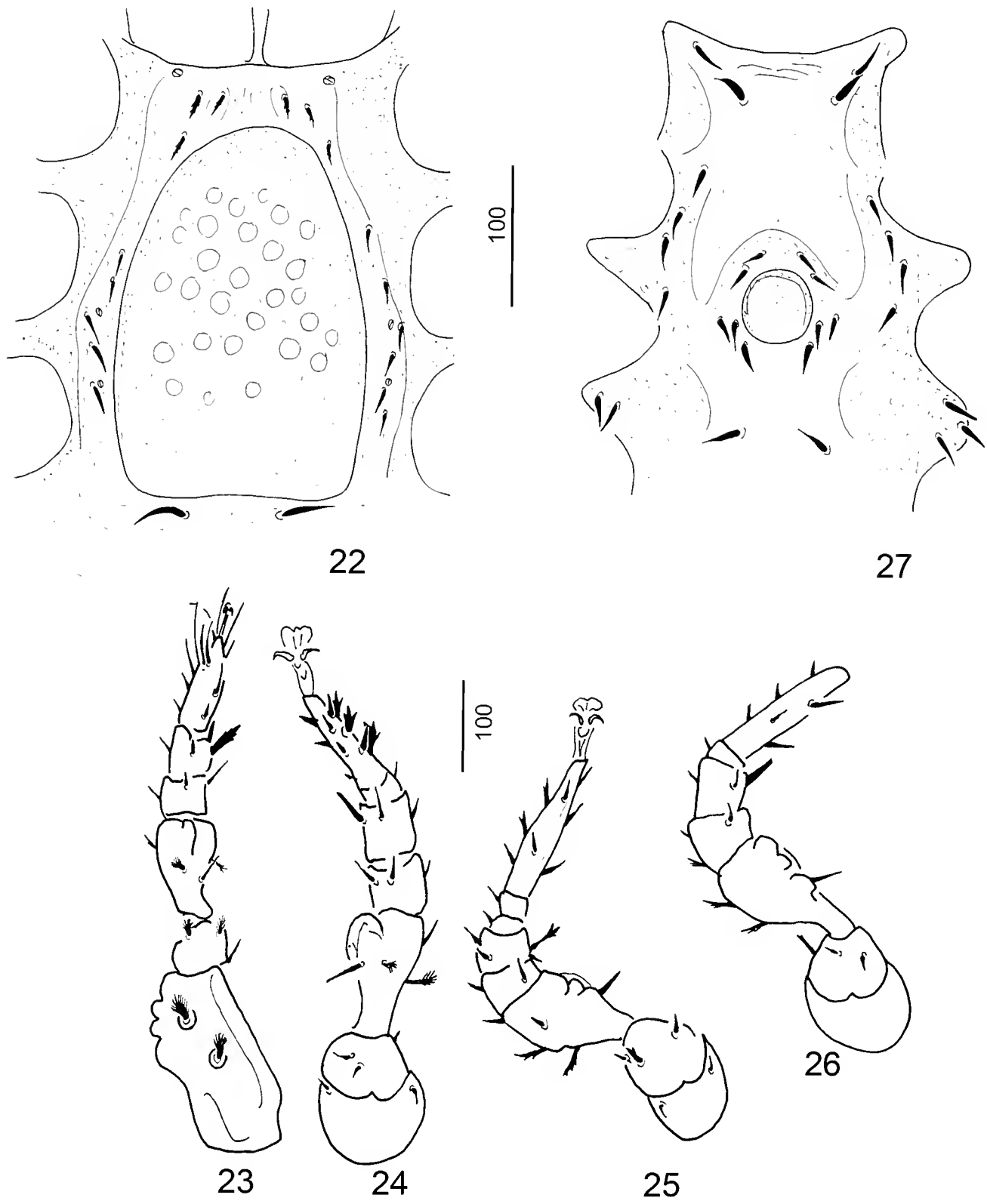
Key to females of the South-East Asian species of trachyuropodid mites

- 1A Dorsal shield without deep pits, depressions or strongly sclerotized structures (grooves, humps, etc.) (Figs 29-30) 2
- 1B Dorsal shield with deep pits, depressions or strongly sclerotized structures (grooves, humps, etc.) (Figs 28, 31-34) 3
- 2A Idiosoma oval, wide and lemon-shaped, anterior area of marginal shield narrow (Fig. 30) (genus *Trachyibana*) *Trachyibana sarawakiensis* Kontschán, 2015
- 2B Idiosoma narrow, anteriorly pointed, anterior part of marginal shield broad (Fig. 29) (genus *Leonardiella*) *Leonardiella cistulata* (Hirschmann, 1975)
- 3A One pair of kidney-shaped lateral depressions situated on dorsal shield (Fig. 28) (genus *Arculatrachys*) *Arculatrachys inuitans* (Berlese, 1905)
- 3B Dorsal shield without pair of kidney-shaped lateral depressions but with strongly sclerotized structures (grooves, humps, etc.) and with a central furrow (Figs 31-34) (genus *Bostocktrachys*) 4
- 4A Four strongly sclerotized longitudinal grooves situated posterior to central transversal furrow (Fig. 33) *Bostocktrachys surinensis* sp. nov.
- 4B Without four strongly sclerotized longitudinal grooves posterior to central transversal furrow 5
- 5A Strongly sclerotized margin of elevated area anterior to transversal furrow in the shape of an inverted omega (Figs 31 and 34) 6
- 5B Strongly sclerotized margin of elevated area anterior to transversal furrow in the shape of a wide and inverted pentagon (Fig. 32) *Bostocktrachys nicherdzinskii* (Hirschmann, 1976)
- 6A Elevated area posterior to transversal furrow recurved-rounded and narrower than elevated area anterior to furrow (Fig. 31) *Bostocktrachys tuberculata* (Berlese, 1913)
- 6B Elevated area posterior to transversal furrow recurved-angular and as wide as elevated area anterior to furrow (Fig. 34) *Bostocktrachys thailandica* sp. nov.

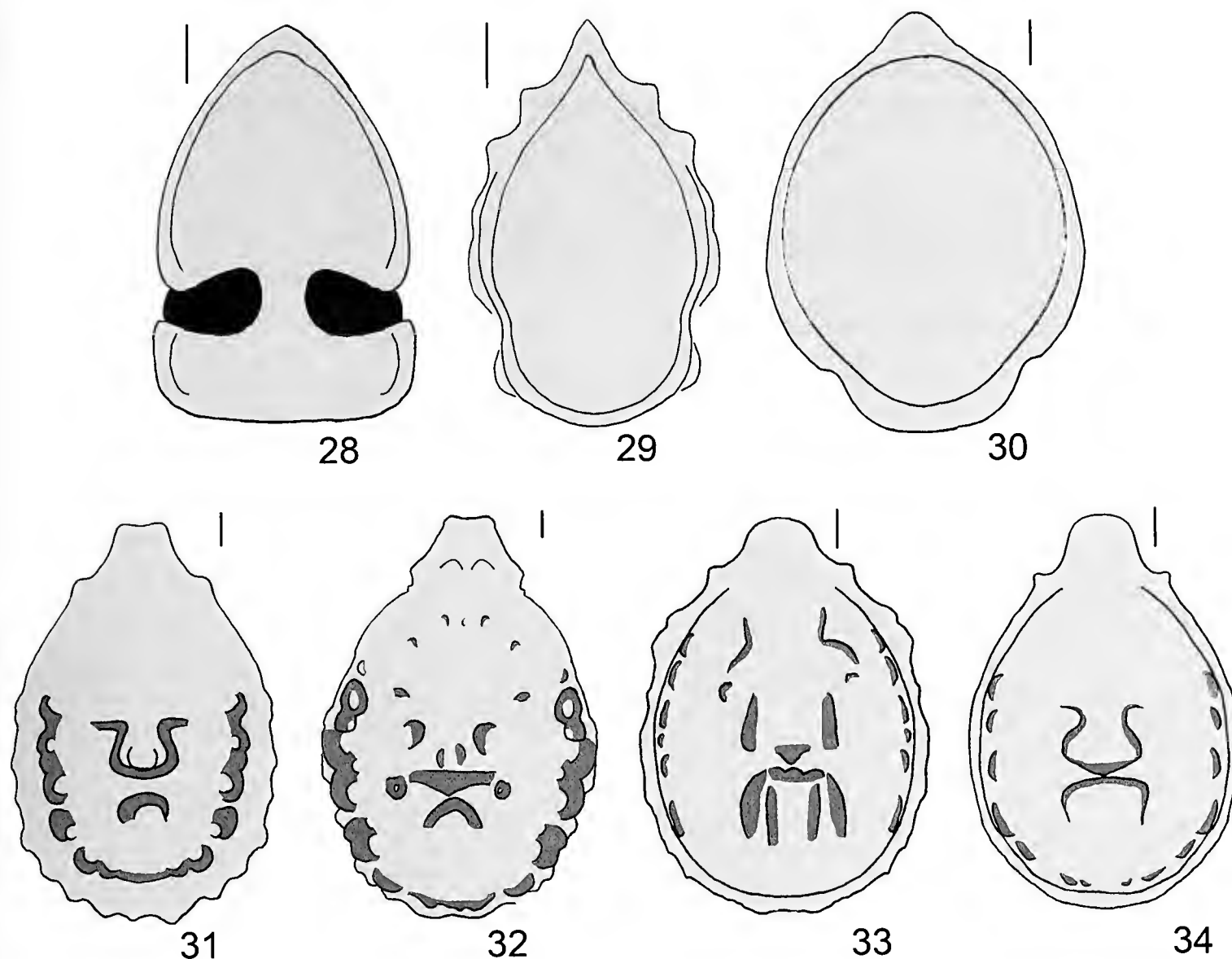
poorly investigated, but judging from the number of known European (see Mařán, 2001) and Neotropical (see Kontschán, 2011c) trachyuropodid species we assume that many more new species from this region will be discovered and described in the future.

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Figs 22-27. *Bostocktrachys thailandica* sp. nov., female holotype (22-26) and male paratype (27). (22) Intercoxal area. (23) Ventral view of leg I. (24) Ventral view of leg II. (25) Ventral view of leg III. (26) Ventral view of leg IV. (27) Intercoxal area of male paratype.



Figs 28-34. Schematic illustrations of dorsal aspect of South-East Asian trachyuropodid mites (Scale bars: 100). (28) *Arculatrachys imitans* (Berlese, 1905). (29) *Leonardiella cistulata* (Hirschmann, 1975). (30) *Trachybana sarawakiensis* Kontschán, 2015. (31) *Bostocktrachys tuberculata* (Berlese, 1913). (32) *Bostocktrachys micherdzinskii* (Hirschmann, 1976). (33) *Bostocktrachys surinensis* sp. nov. (34) *Bostocktrachys thailandica* sp. nov.

the manuscript. Dr Maria L. Moraza (Universidad de Navarra) kindly reviewed the manuscript and suggested additions which led to a major improvement.

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First records of *Hypsugo joffrei* (Thomas, 1915) and the revision of *Philetor brachypterus* (Temminck, 1840) specimens (Chiroptera: Vespertilionidae) from the Indian Subcontinent

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Abstract: The Joffre's pipistrelle *Hypsugo joffrei* is a rare and very little known vespertilionid bat previously thought to be confined to Myanmar and Vietnam in Southeast Asia. Based on recently collected material and reassessment of museum specimens, this species is being reported for the first time from India and Nepal which also significantly extends its westward geographic range beyond Myanmar. We also critically compare the type specimen of another poorly known congener from Myanmar, *H. anthonyi* with the present material and propose to recognize the name *H. anthonyi* as the junior subjective synonym of *H. joffrei*. Specimens previously identified as *Philetor brachypterus* from South Asia were found to represent *H. joffrei*, as well. Consequently, the distribution range of *Philetor* is restricted to the Sundaic zoogeographical subregion, the Philippines, New Guinea and Bismarck Is., and the species should be omitted from the bat checklists of India and Nepal.

Keywords: Chiroptera - Vespertilionidae - India.

INTRODUCTION

The Joffre's Pipistrelle *Hypsugo joffrei* (Thomas, 1915) is a poorly known vespertilionid bat that has previously often been classified in the genus *Pipistrellus* (Corbet & Hill, 1992; Bates *et al.*, 2005). It was designated as Data Deficient by the IUCN (Francis & Bates, 2008). Besides the type specimen from Kachin Hills in northern Myanmar, this bat is known by a few specimens from Sagaing division of Chin state in Myanmar (Bates *et al.*, 2005) and from North Vietnam (Kruskop & Shchinov, 2010; Kruskop, 2013). The distinction of *H. joffrei* from another poorly known taxon from Myanmar, *H. anthonyi* (Tate, 1942), rests on slight colour differences. According to the description, *H. anthonyi* is "a dark brown pipistrelline bat structurally close to *joffrei* but colored very dark brown instead of pale brown" (Tate, 1942). However, Bates *et al.* (2005) who examined the specimens kept in the Natural History Museum, London (formerly British Museum of Natural History, BMNH) and referred to *H. joffrei*, noticed that one of them (BMNH.16.3.26.2) was intermediate in colour, suggesting that *H. anthonyi* may prove to be conspecific with *H. joffrei* (Bates *et*

al., 2005). Based on a recently collected specimen from Shillong in northeastern India and examination of museum specimens, we report here a detailed description of this rare species, revise the records of *Philetor* from Sikkim and Nepal, provide mensural information for all known specimens of *H. joffrei* (except the Vietnamese ones) and compare them with *H. anthonyi* in order to resolve their relationship.

MATERIALS AND METHODS

Specimens were examined externally and measured with a dial caliper to the nearest 0.1 mm, while cranidial measurements were taken to the nearest 0.01 mm, as described in Csorba *et al.* (2011). Acronyms of morphological measurements are as follows: Head and body length (HB); tail length (TAIL); ear length (EAR); tragus length (TRAGUS); hindfoot length, excluding claw (HF); forearm length (FA); tibia length (TIBIA); total length of 3rd digit (DIG3); total length of 4th digit (DIG4); total length of 5th digit (DIG5); greatest length of skull (STOL); condylobasal length

(CBL); condylocanine length (CCL); maxillary toothrow length (CM³L); width across third molars (M³M³W); width across canines (CCW); length of upper molars (M¹M³L); rostral width (lachrymal; ROW); zygomatic width (ZYW); interorbital width (IOW); mastoid width (MAW); width of braincase (BCW); height of braincase (BCH); anteorbital width (from the foramen infraorbitale to the foramen lachrymale; AOB); upper canine–premolar length (CP¹L); length of mandible (ML); mandibular toothrow length (CM₃L); lower canine–premolar length (CP₄L); coronoid height (CPH); length of lower molars (M₁M₃L).

Museum acronyms are: AMNH: The American Museum of Natural History, New York; BM(NH): The Natural History Museum, London, UK, formerly British Museum (Natural History); FMNH: The Field Museum of Natural History, Chicago; MSB: Museum of Southwestern Biology, University of New Mexico, Albuquerque; ZSI: Zoological Survey of India, Shillong.

TAXONOMY

An adult male specimen of *Hypsugo joffrei* was collected in a mist net in the early evening hours of 18th October, 2012 in the Risa Colony area (25°33.566'N 91°53.931'E, ca 1500 m a.s.l.) on the southern part of the Shillong city (State of Meghalaya, India). The collection locality was close to a small stream in the middle of human habitations and adjacent to a park-like forest made up essentially of *Pinus kesiya*. The animal is preserved in alcohol with the skull removed and incorporated in the collections of the Zoological Survey of India, Shillong, under the registration number V/M/ERS/292.

After capture, the individual was kept for a day in captivity for observation. It had noticeably enlarged testis and hence was probably in reproductive stage. It was very calm and hardly made any attempt to fly or bite when handled gently. This animal had a glossy, dark brown dorsal pelage with a slight reddish tinge and the venter was lighter golden brown; the demarcation line between those two parts was rather sharp (Fig. 1). Individual dorsal hairs were uniformly coloured throughout the whole length whereas the ventral hairs had relatively darker basal portion and lighter tips. Wings and patagium were dark brown and essentially naked, except close to the body. The sides of the muzzle between nostrils and eyes appeared swollen and a few long bristles were visible on the sides of the muzzle. The ears were broad and short with rounded tip and roughly matching a right triangle in side profile. The tragus was short and rounded, with a basal lobe, inner margin concave and the outer margin convex (Fig. 2).

The preserved animal has long and narrow wings, much like those of *Nyctalus* spp., with the fifth digit being noticeably reduced (46 mm in total length) when



Fig. 1. Picture of the live adult male *H. joffrei* ZSI V/M/ERS/292. Note the dark brown, glossy appearance of the dorsal pelage, and the sharp demarcation between the dorsal and lighter ventral colour.

compared to the third (66 mm). The plagiopatagium is attached to the middle of the metatarsus. The thumb is short, with a small basal pad and bears a short claw. The calcar along the uropatagium has a distinct lobe. The tail tip projects out of uropatagium by about 2.5 mm. The penis does not possess any special structures and is bristly on the dorsal shaft and the testes appear swollen. Because we could not obtain a specific permission while examining the specimen, we refrained from studying the baculum and conducting further genetic studies.

The skull is rather compact with short and wide rostrum, and short braincase; the supraorbital processes are very prominent and protruding laterally. The braincase is slightly globose and raised posteriorly. The occipital and sagittal crests are hardly developed and do not meet at the lambda. The mandible has a relatively high coronoid process. The two upper incisors are bifid, sub-equal in surface, with the first (I²) being higher than the second (I³). The I³ is placed laterally to the first, and its highest cusp reaches the height of the second cups of I². The upper canines are divergent, strong and slender with a prominent secondary cusp nearly reaching half of the primary cusp. A minute first upper premolar (P²) is present between the canine and second premolar (but not in contact with them) on the right toothrow but is absent on the left one. The second upper premolar (P³) is well developed and about half the length of the canine. The



Fig. 2. Portrait of *H. joffrei* specimen ZSI V/M/ERS/292. Note the enlarged muzzle and short, roundish tragus.

lower canines are long and slender, and lack secondary cusps. The first lower premolar (P_2) is slightly less in height than the second premolar (P_4); both premolars are compressed in the toothrow. Contrary to all true *Pipistrellus* species, the lower molars in our specimen are myotodont which corresponds to the dental configuration found in *Hypsugo* (Horáček & Hanák, 1985-86).

Thomas described *Nyctalus joffrei* (= *H. joffrei*) based on a specimen from Kachin Hills in Upper Burma (Myanmar) (Thomas, 1915). The reason for its original inclusion in the genus *Nyctalus* was the very small first upper premolar and the reduced fifth digit of the wing, although the author noted its morphological resemblance with *Pipistrellus* bats. The type specimen of *H. joffrei* BM(NH) 88.12.1.37 has a uniform pale brown dorsal and ventral pelage (Thomas, 1915). Externally, cranially and dentally, *H. joffrei* closely resembles another very poorly known species *Pipistrellus anthonyi* (= *H. anthonyi*) except for the very dark brown colour of the latter (Tate, 1942; Bates *et al.*, 2005). This species is known only by a male specimen from Changyinku village in the Chipwi River Valley in Myanmar's Kachin State (which is also close to the type locality *H. joffrei*) and is in possession of the American Museum of Natural History, New York. The type specimens of both *H. joffrei* and *H. anthonyi* were examined by one of the authors (GC), and their skulls were sketched (Fig. 3a, b).

The colouration of the well preserved skin of *H. anthonyi* resembles Tate's original description as "firm, glossy

and velvety. Dorsal color near Bone Brown; hairs of underparts tipped with Wood Brown, their bases fuscous" (Tate, 1942). Its plagiopatagium attaches near the middle of the metatarsus and the calcar has an elongated epiblemma seemingly supported by a fine central cartilage. The skull, however, is damaged except for the rostral portion (Fig. 3b); the lower molars are myotodont. The obtainable cranial measurements of the type specimen of *H. anthonyi* are comparable to those of *H. joffrei* (Table 1). However, the colour difference between the two species on the basis of which the species distinction was based seems doubtful as one specimen from west of Kindat, Sagaing Division, in north-western Myanmar [BM(NH).16.3.26.2] assigned to *H. joffrei* is intermediate in colour (Bates *et al.*, 2005). The present specimen caught in Shillong (i.e. less than 400 km west of Kindat) also has a darker dorsal and lighter ventral colouration, thus resembling both *H. anthonyi* and the above referred specimen of *H. joffrei* from Myanmar. It also corresponds very well with the external and mensural characteristics of other known *H. joffrei* specimens (Table 1), including the typically reduced fifth digit, reduced (or absent) P^2 , long bicuspid upper canine and well developed supraorbital processes. Like the Indian specimen, the Vietnamese specimens of *H. cf. joffrei* are also relatively darker in colouration on the dorsum and lighter below (Kruskop & Shchinov, 2010) and this moderate colour variation could be an outcome of individual variations. Thus, we propose to include *H. anthonyi* as a junior synonym of *H. joffrei*.

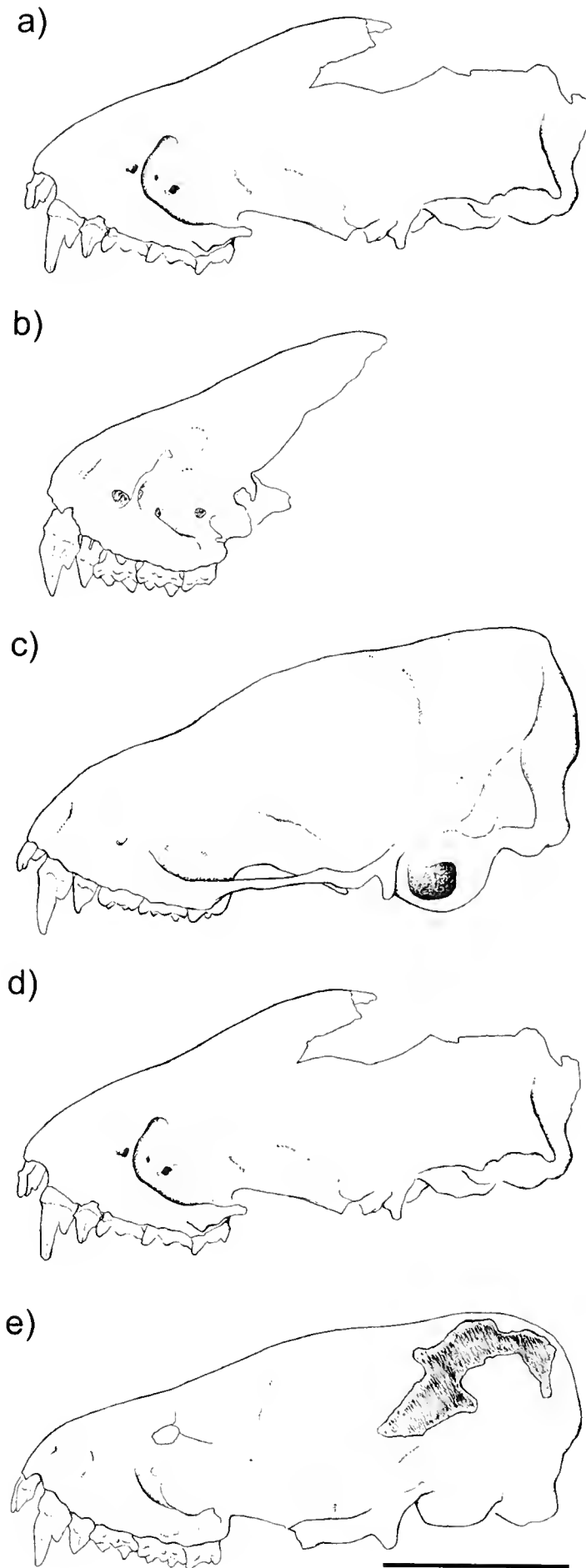


Fig. 3. Lateral views of skulls of (a) *H. joffrei* holotype from Myanmar (BMNH 88.12.1.37), (b) *H. anthonyi* holotype from Myanmar (AMNH 114849), (c) *H. joffrei* from Shillong, Meghalaya (ZSI V/M/ERS/292), (d) *H. joffrei* from Sikkim (MSB 67467), (e) *H. joffrei* from Nepal (FMNH 114249). Scale bar represents 5 mm.

Kruskop and Shchinov (2010) noted that although the external and craniodental characteristics (e.g. myotodont molars) of the Vietnam specimens strongly support their allocation to the genus *Hypsugo*, the baculum shape is different from typical *Hypsugo* and its size is minute. As mentioned above, we could not study the baculum structure of the present Indian specimen or those of the types and thus their allocation to the genus *Hypsugo* is essentially based on the same external and craniodental traits. It is worth to note that the very characteristic bifid upper canine of *H. joffrei* does not occur at any other known species of *Hypsugo*. The exact systematic position of *H. joffrei* itself remains a question of extensive taxonomic reassessment supported by molecular data, which we are lacking at this moment.

The mammal collection of the Museum of Southwestern Biology, University of New Mexico, Albuquerque (MSB), holds two specimens of *Philetor brachypterus* from Sikkim State, India. The female specimens (MSB 67466 and 67467) were collected from the montane forests of Hee-Gyathang (27°30'N 88°30'E, 1846 m a.s.l.) in North Sikkim district and were identified by late Karl Koopman of the American Museum of Natural History. Obviously, based on these specimens, *P. brachypterus* was included in the Indian bat fauna (Molur *et al.*, 2002). Although we could not personally study the above specimens from Sikkim or obtain craniodental measurements, the forearm measurements and photographs on the cranium and dentition taken from the MSB 67467 individual strongly suggest that these specimens do not belong to *Philetor* but indeed, represent *H. joffrei* (Fig. 3d). This identification was based on the following morphological traits: shape of rostrum and shallow basioccipital pits are typical *Hypsugo* (vs. extremely shortened rostrum and very deep basioccipital pits in *Philetor*), normally developed upper incisors (vs. blade-like and shortened I² and very reduced I³), and myotodont lower molars (vs. nyctalodont molars).

Finally, on the basis of two female specimens stored in the Field Museum of Natural History, Chicago, Koopman also reported the presence of *P. brachypterus* from Eastern Nepal which has subsequently been retained in the Nepalese faunal lists (Koopman, 1983; Molur *et al.*, 2002; Jnawali *et al.*, 2011; Thapa, 2014). The FMNH 114249 and 114481 specimens were collected from Bahrabise in Sindhupalchok district of Central Nepal (approx. 27°78'N 85°89'E, 575 m a.s.l.) and Num Bridge (approx. 27°54'N 87°34'E, 850 m a.s.l.) in Sankhuwasabha district of Eastern Nepal, respectively. These specimens were physically examined by one of the authors (GC) and clearly, the Nepalese specimens do not belong to the genus *Philetor* as reported by Koopman (1983), rather concur well with all the generic characteristics of *Hypsugo*, especially in the unmodified external genitalia and myotodont lower molars. The external, cranial (Fig. 3e) and mensural characteristics (Table 1) of the FMNH specimens conform to the

Table 1. The external and cranial measurements (in mm) of *H. joffrei* specimens from India, Nepal and Myanmar including the holotypes. Measurements marked with * are taken from Tate (1942).

Character	Shillong specimen ZSI V/M/ ERS/292	Nepal specimens FMNH 114249, 114481	Sikkim specimens MSB 67466, 67467	Burmese specimens BM(NH) 16.3.26.2, 16.3.26.83, 16.3.26.84	<i>H. joffrei</i> holotype BM(NH) 88.12.1.37	<i>H. anthonyi</i> holotype AMNH 114849
HB	61	-	-	-	-	-
TAIL	37	-	-	-	-	41*
EAR	13.2	-	-	-	-	-
TRAGUS	5.1	-	-	-	-	-
HF	8.3	7.2	-	-	-	10*
FA	40.2	37.8, 38.6	38.0-38.5	-	38.8	38*
TIBIA	15.6	15.8	-	-	-	12*
DIG3	66	-	-	-	-	-
DIG4	57.5	-	-	-	-	-
DIG5	46	-	-	-	-	-
STOL	15.1	15.77	-	-	-	-
CBL	14.8	-	-	-	-	-
CCL	13.98	14.33	-	-	-	-
CM3L	5.18	5.15	-	5.13	5.15	-
M³M³W	7.23	6.99	-	-	-	-
CCW	5.01	5.14	-	-	-	-
M¹M³L	3.60	-	-	-	-	-
ROW	7.80	6.84	-	8.18-8.59	7.70	7.92
ZYW	10.09	-	-	10.44	-	-
IOW	4.70	4.83	-	4.72-4.86	4.55	5.02
MAW	9.20	-	-	8.88-9.24	8.92	-
BCW	7.96	8.29	-	7.92-8.30	8.08	-
BCH	5.90	-	-	5.42	-	-
AOB	-	0.36	-	0.75-0.83	0.86	-
CP⁴L	2.00	2.10	-	2.01	2.07	2.18
ML	10.90	11.09	-	10.81-11.17	10.84	10.92
CM₃L	5.29	5.49	-	5.60-5.65	5.52	5.60
CP₄L	1.78	1.80	-	-	-	-
CPH	3.8	3.57	-	3.60-3.77	3.68	-
M₁M₃L	3.8	-	-	-	-	-

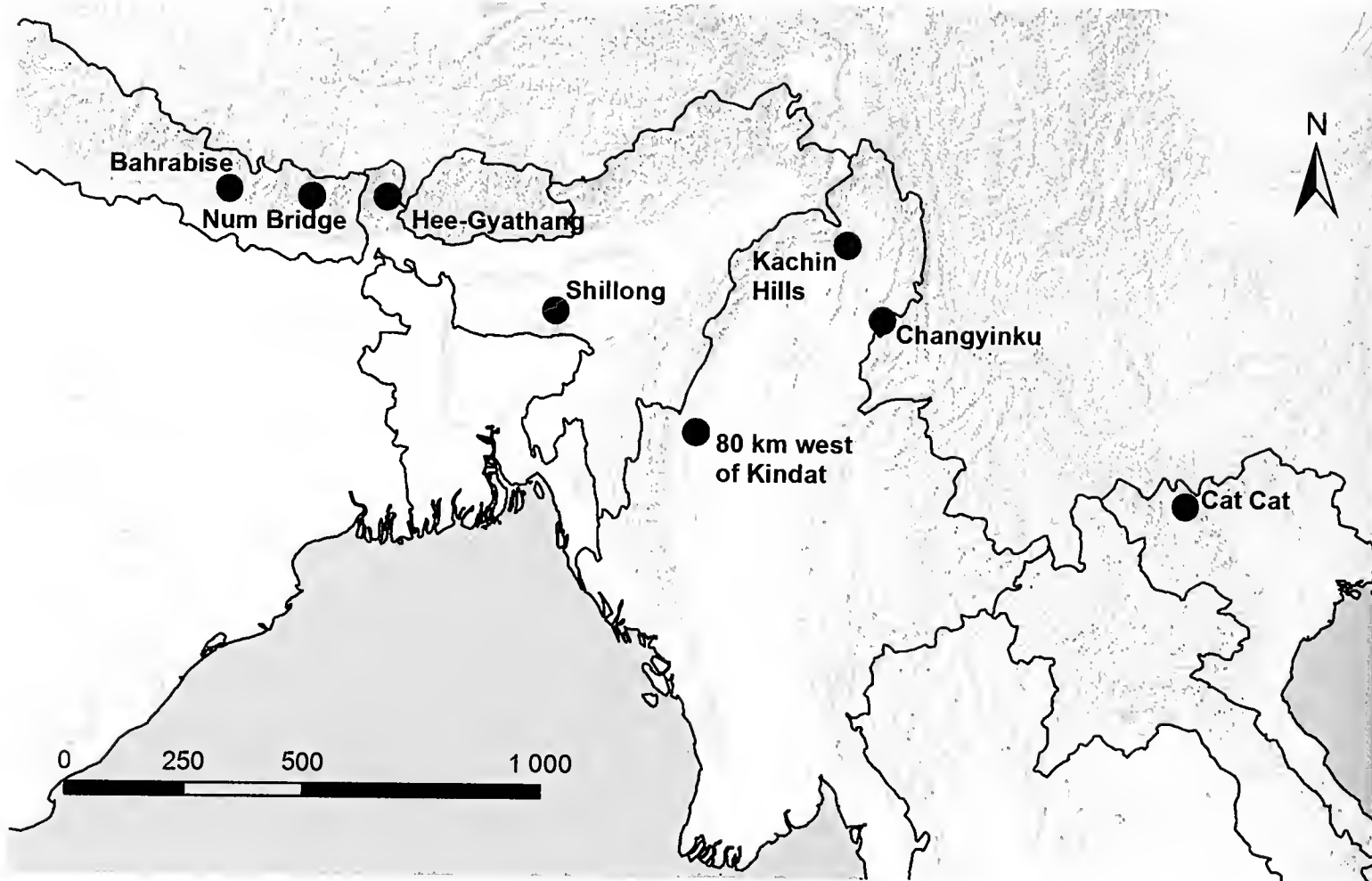


Fig. 4. Map representation of the known occurrences of *H. joffrei*.

described features of *H. joffrei* as well and we therefore revise the Nepalese records of *P. brachypterus* (*sensu* Koopman, 1983) and recognize them as *H. joffrei*.

This study significantly extends the westward distribution range of *H. joffrei* to Central Nepal through northeastern India by over 900 km from the previously known localities in Myanmar, and thus represent the first records of the species in India and Nepal (Fig. 4). The area where the Meghalaya specimen was caught suggests that this apparently rare species might be tolerant to more disturbed habitats than anticipated and could be found in other regions on the foothills of the Himalaya, which are part of the Indo-Burma biodiversity hotspot (Myers *et al.*, 2000). In northern Vietnam, this bat is seemingly not uncommon in some areas of Lao Cai Province (Kruskop & Shchinov, 2010) and may not be as rare in other parts of its distribution range as thought previously. With these revised records, the bat diversity within the political boundary of India and Nepal currently stands at 124 and 51 species respectively (Talmale & Pradhan, 2009; Ruedi *et al.*, 2012; Ruedi *et al.*, 2013; Senacha & Dookia, 2013; Thapa, 2014).

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Adult Trematodes (Platyhelminthes) of freshwater fishes from Argentina: a checklist

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Abstract: This work provides information on the occurrence of adult trematodes (Aspidogastrea and Digenea) in freshwater fishes from Argentina. To date, a total of 77 trematode species belonging to 21 families have been recorded. Haploporidae, Allocreadiidae and Cryptogonimidae (15, nine and nine species, respectively) showed the highest species richness, whereas the number of species ranged from one to seven species for the other 18 families. Of these, five new species have been recently described in Argentina; nine were cited for the first time; 17 had new host records, and 28 were reported from new localities. The orders Characiformes, Perciformes and Siluriformes harboured the highest richness of trematode species.

Keywords: Biodiversity - Aspidogastrea - Digenea - New hosts - First records - New localities.

INTRODUCTION

The first study of Trematoda of freshwater fishes in Argentina was conducted by Szidat (1951), and since then several new species have been described. Since the study of South-American trematodes by Kohn *et al.* (2007) and other work of parasites restricted to the middle Paraná River (Chemes & Takemoto, 2011), 15 new species of freshwater fish trematodes have been described and/or recorded for this region, making a total of 199 fully identified species at the adult stage. Recently, an attempt was made to provide a worldwide overview on freshwater fish trematodes (Choudhury *et al.*, 2016; Scholz *et al.*, 2016).

The freshwater fish fauna of Argentina consists of more than 500 species, with new species being constantly described (Menni, 2004; Cussac *et al.*, 2009; Almirón *et al.*, 2008, 2015; Mirande & Koerber, 2015).

The objective of the present checklist is to update the diversity of adult trematodes from freshwater fishes from Argentina. It is based on published papers cited in the references, and records of species cited for the first time or that were found in new hosts and localities, which were obtained by the authors during the last 26 years.

MATERIAL AND METHODS

The checklist is based upon published papers between 1951 and 2016. The Trematoda are presented according to families in alphabetical order; each taxon contains information on the species such as authority and year, synonyms, acronyms of museums for the deposited material, host(s) (including type host and country), localities (including type locality and country), site of infection, life cycle (when it is completely known), references and remarks (when justified). A list of fish hosts and their trematodes is also included. The classification for trematodes follows the Keys to the Trematoda (Gibson *et al.*, 2002; Jones *et al.*, 2005; Bray *et al.*, 2008) and the fish classification is according Fishbase (Froese & Pauly, 2016).

Acronyms for the helminthological collections are: BMNH - British Museum of Natural History, London, United Kingdom; CHIOC - Helminthological Collection of the Oswaldo Cruz Institute, Rio de Janeiro, Brazil; IPCAS - Institute of Parasitology, Academy of Science of the Czech Republic, České Budějovice, Czech Republic; MACN-Pa - Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires, Argentina; MLP

- Museo de La Plata, Buenos Aires, Argentina; NHM - Naturhistorisches Museum Wien, Vienna, Austria; NSMT-PI - National Science Museum, Tokyo, Japan [now National Museum of Nature and Science (NMNS)]; NRM - Swedish Museum of Natural History, Stockholm, Sweden; UNC - Parasite Collection of the Universidad Nacional del Comahue, Bariloche, Argentina; USNM - United States National Parasite Collection, Washington, U.S.A [recently transferred to the National Museum of Natural History (NMNH)]. Deposition numbers at MACN are indicated only for new voucher material. The following abbreviations and symbols are used: *new host registered by the present authors; **new locality registered by the present authors; ● indicated doubtful fish host; IH1, first intermediate host; IH2, second intermediate host; and FH, final host.

RESULTS

Class Trematoda Rudolphi, 1808

Subclass Aspidogastrea Faust & Tang, 1936

Family Aspidogastridae Poche, 1907

Lobatostoma Eckmann, 1932

Lobatostoma jungwirthi Kritscher, 1974

Material deposited: MACN-Pa 582/1–5 (new voucher material), MLP, NHM (type material).

Hosts: *Gymnogeophagus rhabdotus* (Hensel) (= *Geophagus brachyurus* Cope) (type host, Brazil), *Australoheros facetus* (Jenyns) [= *Cichlasoma facetum* (Jenyns)] (Perciformes: Cichlidae).

Life cycle: IH1 *Heleobia castellanosa* Gaillard, *Heleobia parchappii* (d'Orbigny) (Gastropoda: Rissooidea) (natural hosts); FH *A. facetus* (natural host), *Gymnogeophagus meridionalis* Reis & Malabarba (experimental host).

Localities: Rio dos Sinos (San Leopoldo), Rio Grande do Sul State, Brazil (type locality); Cantera (quarry) (Berisso), Chascomús Lagoon (Chascomús) and Saladita Pond (Avellaneda), Buenos Aires Province; Tres de Febrero Park (artificial pond), Buenos Aires City.

Site of infection: Gonads and digestive gland in the molluscan host, posterior intestine and rectum in the cichlid fishes.

References: Kritscher (1974) Lunaschi (1984a), Zylber & Ostrowski de Núñez (1999), Paola & Damborenea (2001).

Remarks: Some specimens began egg production in the molluscan host. Paola & Damborenea (2001) studied the tegument surface of the species.

Subclass Digenea Carus, 1863

Family Allocreadiidae Looss, 1902

Allocreadium Looss, 1900

Allocreadium patagonicum Shimazu, Urawa & Coria, 2000

Polylekithum percai Ostrowski de Núñez, Brugni & Viozzi, 2000

Material deposited: BNMH, IPCAS (type material), MACN-Pa, NSMT-PI (type material); UNC.

Hosts: *Percichthys colhuapiensis* (MacDonagh) (type host), *Percichthys trucha* (Valenciennes) (Perciformes: Percichthyidae).

Locality: Aluminé Lake (type locality), Neuquén Province; Falkner, Moreno and Escondido Lakes, Río Negro Province; Rivadavia Lake, Chubut Province.

Site of infection: Intestine.

References: Ostrowski de Núñez *et al.* (2000), Shimazu *et al.* (2000), Flores *et al.* (2004).

Remarks: Ostrowski de Núñez *et al.* (2000) described *P. percai* from *P. trucha* in Patagonia; posteriorly Flores *et al.* (2004) considered this species as synonym of *A. patagonicum*.

Allocreadium pichi Flores, Brugni & Ostrowski de Núñez, 2004

Material deposited: BMNH (type material), MACN-Pa (type material), MLP (type material), UNC (type material).

Hosts: *Galaxias maculatus* (Jenyns) (type host) (Osmeriformes: Galaxiidae).

Locality: Moreno Lake, Río Negro Province (type locality).

Site of infection: Intestine.

Reference: Flores *et al.* (2004).

Auriculostoma Scholz, Aguirre-Macedo & Choudhury, 2004

Auriculostoma macrorchis (Szidat, 1954)

Crepidostomum macrorchis Szidat, 1954

Material deposited: MACN-Pa 583, 584/1–2, 585/1–3, 586/1–2 (type and new voucher material).

Hosts: *Pachyurus bonariensis* Steindachner (type host) (Perciformes: Scienidae); *Ageneiosus inermis* (Linnaeus), *Ageneiosus militaris** Valenciennes, *Auchenipterus nigripinnis* (Boulenger), *Auchenipterus osteomystax* (Miranda Ribeiro) [= *Auchenipterus nuchalis* (Spix and Agassiz)] (Siluriformes: Auchenipteridae), *Luciopimelodus pati** (Valenciennes) (Siluriformes:

Pimelodidae), *Rhinodoras dorbignyi** (Kner) (Siluriformes: Doradidae).

Localities: La Plata River, Buenos Aires City (type locality); Middle Paraná River, Corrientes Province; Colastiné River** (tributary of the Paraná River) (31°40'S, 60°46'W), Santa Fe Province; Paraná-Guazú River** (33°54'S; 58°52'W), Entre Ríos Province.

Site of infection: Anterior, middle and posterior part of intestine.

References: Szidat (1954), Hamann (1988), Scholz *et al.* (2004), Arredondo (2013).

Remarks: New hosts and localities records. Hamann (1988) indicated the presence of *A. macrorchis* in *A. nuchalis*, but according to Liotta (2005) and to Froese & Pauly (2016), the records of this species probably correspond to *A. osteomystax*.

Auriculostoma platense (Szidat, 1954)

Crepidostomum platense Szidat, 1954

Material deposited: MACN-Pa 587, 588/1–2, 589 (type and new voucher material).

Hosts: *Iheringichthys labrosus* (Lütken), *Pimelodus maculatus* Lacépède (= *Pimelodus clarias* Lacépède) (Siluriformes: Pimelodidae) and *Rhinodoras dorbignyi* (Siluriformes: Doradidae) (type host not assigned); *Pimelodus albicans** (Valenciennes), *Pimelodus argenteus** Perugia (Siluriformes: Pimelodidae), *Rhamphichthys rostratus** (Linnaeus) (Gymnotiformes: Rhamphichthyidae).

Localities: La Plata River, Buenos Aires City (type locality); Colastiné River** (tributary of the Paraná River), Santa Fe Province.

Site of infection: Intestine.

References: Szidat (1954), Scholz *et al.* (2004), Arredondo (2013).

Remarks: New hosts and locality records.

Creptotrema Travassos, Artigas & Pereira, 1928

Creptotrema creptotrema Travassos, Artigas & Pereira, 1928

Material deposited: CHIOC (type material), MACN-Pa 590/1–2 (new voucher material), MLP.

Hosts: *Leporinus elongatus* Valenciennes (type host, Brazil), *Leporinus obtusidens* (Valenciennes) (Characiformes: Anostomidae); *Trachelyopterus striatulus** (Steindachner), *Trachelyopterus galeatus* (Linnaeus) (= *Parauchenipterus galeatus* Linnaeus) (Siluriformes: Auchenipteridae).

Localities: Mogi-Guaçu River (Emas, Pirassununga), São Paulo State, Brazil (type locality); Middle Paraná River, Corrientes Province; Colastiné River**, Santa Fe Province; Irigoyen Canal, Talavera Island, Buenos Aires Province.

Site of infection: Anterior part of intestine.

References: Kohn (1984), Lunaschi (1985a), Hamann (1988), Lunaschi & Sutton (1995), Arredondo (2013).

Remarks: New host and locality records.

Creptotrema lynchi Brooks, 1976

Material deposited: MLP, USNM (type material).

Hosts: *Rhinella marina* (Linnaeus) (Anura: Bufonidae) (type host, Colombia), *Leporinus obtusidens*.

Localities: 1 km north of San Cristobal, Atlántico, Colombia (type locality); Irigoyen Canal, Talavera Island, Buenos Aires Province.

Site of infection: Pyloric caeca (in fish).

Reference: Lunaschi & Sutton (1995).

Remarks: The absence of subsequent reports of *C. lynchi* from anurans suggests that *R. marina* may have been an accidental host (Curran, 2008).

Creptotrema pati Lunaschi, 1985

Material deposited: MLP (type material).

Hosts: *Luciopimelodus pati* (type host).

Locality: Atalaya (Magdalena), Buenos Aires Province (type locality).

Site of infection: Intestine.

Reference: Lunaschi (1985a).

Creptotrematina Yamaguti, 1974

Creptotrematina dispar (Freitas, 1941)

Creptotrema dispar Freitas, 1941

Material deposited: CHIOC (type material); not available for Argentinean material.

Host: *Triportheus paranensis* (Günther) (= *Chalcinus paranensis* Günther) (type host, Brazil) (Characiformes: Triportheidae).

Locality: Rio Miranda (Salobra), Mato Grosso State, Brazil (type locality); Middle Paraná River, Corrientes Province.

Site of infection: Anterior part of intestine.

References: Freitas (1941b), Hamann (1988).

Creptotrematium dissimilis* (Freitas, 1941)Creptotrema dissimilis* Freitas, 1941**Material deposited:** CHIOC (type material), MLP.**Host:** *Tetragonopterus argenteus* Cuvier (type host, Brazil); *Astyanax bimaculatus* (Linnaeus), *Astyanax eigenmanniorum* (Cope) (Characiformes: Characidae).**Locality:** Rio Miranda (Salobra), Mato Grosso State, Brazil (type locality); Trin Lagoon (Iberá Inlet), Corrientes Province; Boca Cerrada and Miguelín Stream (Ensenada), Buenos Aires Province.**Site of infection:** Intestine.**References:** Freitas (1941c), Hamann (1983), Lunaschi (1985a).**Alloglossidiidae Hernandez-Mena, Mendoza-Garfias, Ornelas-Garcia & Perez-Ponce de Leon, 2016*****Magnivitellinum* Kloss, 1966*****Magnivitellinum corvitellinum* Lacerda, Takemoto & Pavanelli, 2009****Material deposited:** CHIOC (type material), MACN-Pa 611/1–2 (new voucher material), USNPC (type material).**Host:** *Hoplosternum littorale* (Hancock) (Siluriformes: Callichthyidae) (type host, Brazil).**Localities:** Upper Paraná River floodplain, Brazil (type locality); Paraná-Guazú River**, Entre Ríos Province.**Site of infection:** Middle and posterior part of intestine.**References:** Lacerda *et al.* (2009), Arredondo (2013).**Remarks:** First mention of this species in Argentina.***Magnivitellinum simplex* Kloss, 1966****Material deposited:** MLP, MACN-Pa 612 (new voucher material).**Hosts:** *Astyanax bimaculatus* (type host, Brazil), *Astyanax* sp., *A. eigenmanniorum*, *A. fasciatus*, *Oligosarcus jenynsi*, *Sorubim lima**.**Life cycle:** IH1 *Biomphalaria tenagophila* (d'Orbigny), IH2 *Aedes aegypti* (Linnaeus) (experimental host).**Localities:** Mogi-Guaçu River (Emas, Pirassununga) Estado São Paulo State, Brazil (type locality); Tres Palmeras, Salta Province; Colastiné River** (tributary of the Paraná River), Santa Fe Province; Doña Flora Stream (tributary of La Plata River), Miguelín Stream (Ensenada), Cantera (quarry) Aprilito, Chascomús Lagoon (Chascomús) and La Plata River, Buenos Aires Province.**Site of infection:** Intestine.**References:** Lunaschi (1989b), Arredondo (2013), Davies (2014).**Remarks:** New host and locality record.**Family Apocreadiidae Skrjabin, 1942*****Crassicutis* Manter, 1936*****Crassicutis cichlasomae* Manter, 1936****Material deposited:** MACN-Pa 591/1–2, 592 (new voucher material).**Host:** *Cichlasoma mayorum* Hubbs (type host, México), *Cichlasoma dimerus** (Heckel), *Crenicichla lepidota** Heckel (Perciformes: Cichlidae).**Locality:** Cenote, Yucatán, México (type locality); Colastiné River** (tributary of Paraná River), Santa Fe Province.**Site of infection:** Intestine.**References:** Fernandes & Kohn (2001), Arredondo (2013).**Remarks:** First record of this species in Argentina.***Crassicutis intermedius* (Szidat, 1954)***Eocreadium intermedium* Szidat, 1954**Material deposited:** MACN-Pa 593/1–2 (type and new voucher material).**Host:** *Hypostomus commersoni* (Valenciennes) [= *Plecostomus commersoni* (Valenciennes)] (type host) (Siluriformes: Loricariidae).**Localities:** La Plata River, Buenos Aires City (type locality); Paraná-Guazú River**, Entre Ríos Province.**Site of infection:** Stomach.**References:** Szidat (1954), Arredondo (2013).**Remarks:** New locality record. Bray *et al.* (1996) redescribed this species from *Hypostomus cochliodon* (Kner) and *Hypostomus commersoni*, Paraná River (Itapúa Province) and *Hypostomus piratani* Weber, Santa Sofía Ranch, Concepción Province, Paraguay.***Homalometron* Stafford, 1904*****Homalometron papilliferum* (Szidat, 1956)***Austrocreadium papilliferum* Szidat, 1956**Material deposited:** MACN-Pa (type material), NSMT-PI, UNC.**Host:** *Percichthys trucha* (type host).**Localities:** Limay River, Río Negro Province (type locality); Araucarian Region of Andean Patagonia (see

table 2 in Ostrowski de Núñez *et al.*, 2000), Aluminé Lake, Neuquén Province.

Site of infection: Intestine.

References: Szidat (1956b), Ostrowski de Núñez *et al.* (2000), Shimazu *et al.* (2000).

***Homalometron pseudopallidum* Martorelli, 1986**

Material deposited: MLP (type material).

Host: *Gymnogeophagus australis* (Eigenmann) (Perciformes: Cichlidae) (type host).

Life cycle: IH1 *Heleobia parchappii*; IH2 Tubificidae.

Locality: small lagoon at Los Talas (Berisso), Buenos Aires Province (type locality).

Site of infection: Intestine.

Reference: Martorelli (1986).

***Posterotestes* Ostrowski de Núñez, Brugni & Flores, 2003**

***Posterotestes unelen* Ostrowski de Núñez, Brugni & Flores, 2003**

Material deposited: IPCAS (type material), MACN-Pa (type material), MLP (type material), UNC (type material).

Host: *Percichthys trucha* (type host).

Localities: Epuyén Lake (type locality), Chubut Province; other localities see table 1 in Ostrowski de Núñez *et al.* (2003).

Site of infection: Posterior part of intestine.

Reference: Ostrowski de Núñez *et al.* (2003).

***Procaudotestis* Szidat, 1954**

***Procaudotestis uruguayensis* Szidat, 1954**

Material deposited: BMNH; MACN-PA (type material); MHNG.

Host: *Paraloricaria vetula* (Valenciennes) [= *Loricaria vetula* (Valenciennes)] (type host) (Siluriformes: Loricariidae).

Locality: Uruguay River, Santo Tomé, Corrientes Province (type locality).

Site of infection: Stomach.

Reference: Szidat (1954).

Remarks: Bray *et al.* (1996) redescribed this species from *Loricaria* sp., Paraná River (Itapúa Province), Paraguay.

Family Aporocotylidae Odhner, 1912

***Plehnella* Szidat, 1951**

***Plehnella coelomicola* Szidat, 1951**

Material deposited: MACN-Pa 614/1–2 (type and new voucher material), MLP.

Hosts: *Iheringichthys labrosus* (type host), *Pimelodus albicans*, *P. maculatus*, *Pseudoplatystoma corruscans**, *Hoplosternum littorale**.

Localities: La Plata River in front of Buenos Aires City (type locality), Paraná River**, Italia Port, Corrientes City, Corrientes Province, Paraná-Guazú River**, Entre Ríos Province, Argentina.

Site of infection: Coelomic cavity.

References: Szidat (1951), Lunaschi (1985b), Avendaño de MacIntosh & Ostrowski de Núñez (1998), Arredondo (2013), Orélis-Ribeiro & Bullard (2015).

Remarks: New hosts and localities records. Erroneously referred to as *P. coelomica* by Lunaschi (1985b) and Avendaño de MacIntosh & Ostrowski de Núñez (1998).

***Sanguinicola* Plehn, 1905**

Janickia Rašín, 1928

***Sanguinicola argentinensis* Szidat, 1951**

Material deposited: MACN-Pa (type material).

Hosts: *Prochilodus lineatus* Valenciennes (= *Prochilodus platensis* Holmberg) (type host) (Characiformes: Prochilodontidae).

Localities: La Plata River, Buenos Aires (type locality).

Site of infection: Heart, arteries.

Reference: Szidat (1951).

Family Bucephalidae Poche, 1907

***Prosorhynchoides* Dollfus, 1929**

***Prosorhynchoides cambapuntaensis* Lunaschi, 2004**

Material deposited: MLP (type material).

Host: *Salminus brasiliensis* (Cuvier) (= *Salminus maxillosus* Valenciennes) (type host) (Characiformes: Bryconidae).

Locality: Paraná River near Experimental Field Cambá-Punta, Corrientes Province (type locality).

Site of infection: Intestine.

Reference: Lunaschi (2004).

Prosorhynchoides rioplatensis* (Szidat, 1970)Bucephalopsis rioplatensis* Szidat, 1970**Material deposited:** MACN-Pa (type material).**Host:** *Catathyrindium jenynsii* (Günther) (= *Achirus trichospilus* Berg) (type host) (Pleuronectiformes: Achiridae).**Locality:** La Plata River, Buenos Aires City (type locality).**Site of infection:** Intestine.**References:** Szidat (1970b), Lunaschi (2003).***Rhipidocotyle* Diesing, 1858*****Rhipidocotyle santanaensis* Lunaschi, 2004****Material deposited:** MLP (type material).**Host:** *Acestrorhynchus pantaneiro* Menezes (type host) (Characiformes: Acestrorhynchidae).**Locality:** Small natural pond at Santa Ana (type locality), Corrientes Province.**Site of infection:** Pyloric caeca.**Reference:** Lunaschi (2004).**Family Callodistomidae Odhner, 1910*****Prosthenthystera* Travassos, 1922*****Prosthenthystera obesa* (Diesing, 1850)***Distomum obesum* Diesing, 1850*Pseudoprosthenthystera microtesticulata* Kloss, 1966**Material deposited:** MLP, NHM (type material).**Hosts:** *Salminus brasiliensis* (= *S. brevidens* Cuvier), *Leporinus friderici* (Bloch) (type host not assigned, Brazil) (Characiformes: Anostomidae), *Luciopimelodus pati**, *Pimelodus albicans**.**Localities:** Mato Grosso State, Brazil (type locality); Colastiné River** (tributary of Paraná River), Santa Fe Province; Delta of Paraná River, Buenos Aires Province; Irigoyen Canal, Talavera Island, Buenos Aires Province; La Plata River** in front of Buenos Aires City.**Site of infection:** Gall bladder.**References:** Diesing (1950), Lunaschi & Sutton (1995), Arredondo (2013).**Remarks:** New hosts and locality records. Kohn *et al.* (1997) redescribed this species from Brazil parasitizing a wide range of hosts.**Family Cladorchiidae Southwell & Kirshner, 1937*****Dadaytrema* Travassos, 1931*****Dadaytrema gracilis* Lunaschi, 1989****Material deposited:** MACN-Pa 594/1–2 (new voucher material), MLP (type material).**Hosts:** *Pimelodella gracilis* (Valenciennes) (type host) (Siluriformes: Heptapteridae), *Pterodoras granulosus** (Valenciennes) (Siluriformes: Doradidae).**Localities:** Brazo Chico Stream (tributary of Uruguay River), Entre Ríos Province (type locality), Paraná-Guazú River**, Entre Ríos Province.**Site of infection:** Middle and posterior part of intestine.**References:** Lunaschi (1989a), Arredondo (2013).**Remarks:** New host and locality records. The present authors also recovered *D. gracilis* in the type host.***Dadaytrema oxycephala* (Diesing, 1836)***Amphistoma oxycephalum* Diesing, 1836*Dadayia oxycephala* Travassos, Artigas & Pereira, 1928**Material deposited:** MACN-Pa 595 (new voucher material), NHM (type material).**Hosts:** *Salminus brasiliensis* (*Salmo aurata* Larrañaga), *Salmo pacu* (non valid name), *Silurus megacephalus* (non valid name) and *Myleus rhomboidalis* (Cuvier) (*Salmo pacupeba* Kner) (type host not assigned, Brazil), *Piaractus mesopotamicus* (Holmberg) (Characiformes: Serrasalminae), *Pterodoras granulosus*.**Localities:** Paraná River, Cuyaba, Araguay River, Brazil (type locality); Paraná and Paraguay rivers confluence and Middle Paraná River near Corrientes City, Corrientes Province; Colastiné River** (tributary of Paraná River), Santa Fe Province; Paraná-Guazú River**, Entre Ríos Province.**Site of infection:** Middle and posterior part of intestine.**References:** Hamann (1982a, b), Arredondo (2013).**Remarks:** New locality records.***Dadaytremoides* Thatcher, 1979*****Dadaytremoides parauchenipteri* Lunaschi, 1989****Material deposited:** MLP (type material).**Host:** *Trachelyopterus galeatus* (Linnaeus) [= *Parauchenipterus galeatus* (Linnaeus)] (type host) (Siluriformes: Auchenipteridae).**Locality:** Brazo Chico Stream (tributary of Uruguay River), Entre Ríos Province (type locality); Yrigoyen Canal, Talavera Island, Buenos Aires Province.**Site of infection:** Intestine.

References: Lunaschi (1989a), Lunaschi & Sutton (1995).

***Microorchis* Daday, 1907**

***Microorchis oligovitellinum* Lunaschi, 1987**

Material deposited: MACN-Pa 596, 597 (new voucher material), MLP (type material).

Hosts: *Luciopimelodus pati* and *Trachelyopterus striatulus* [= *Trachycoristes striatulus* (Steindachner)] (type host not assigned), *Ageneiosus inermis**, *A. militaris**, *Pterodoras granulosus**.

Localities: Atalaya (Magdalena) and Punta Lara (Ensenada), Buenos Aires Province (type locality not assigned); Colastiné River** (tributary of Paraná River), Santa Fe Province.

Site of infection: Anterior, middle and posterior part of intestine.

References: Lunaschi (1987), Arredondo (2013).

Remarks: New hosts and locality records.

***Travassosinia* Vaz, 1932**

***Travassosinia dilatata* (Daday, 1907)**

Chiorchis dilatatus Daday, 1907

Material deposited: MACN-Pa 598 (new voucher material), information about type material not provided by Daday (1907).

Hosts: *Piaractus brachipomus* (Cuvier) [= *Colossoma brachypomus* (Cuvier)] (type host, Paraguay), *P. mesopotamicus* [= *Colossoma mitrei* (Berg)] (Characiformes: Serrasalminidae), *P. granulosus*, *Salminus brasiliensis**.

Localities: Paraguay (type locality); Paraná and Paraguay rivers confluence and Middle Paraná River near Corrientes City, Corrientes Province; Paraná-Guazú River**, Entre Ríos Province.

Site of infection: Intestine.

References: Daday (1907), Hamann (1982a, b), Arredondo (2013).

Remarks: New host and locality records. The description of this species was based on one specimen from Paraguay; it was not possible to trace where this specimen was deposited.

Family Cryptogonimidae Ward, 1917

***Acanthostomoides* Szidat, 1956**

***Acanthostomoides apophalliformis* Szidat, 1956**

Material deposited: IPCAS, MACN-Pa (type material), NSMT-PI, UNC.

Hosts: *Percichthys trucha* (type host), *P. collnapiensis*, *Galaxias maculatus*, *Oncorhynchus mikiss* (Walbaum), *Salmo trutta* (Linnaeus) (Salmoniformes: Salmonidae), *Olivaichthys viedmensis* (MacDonagh) (= *Diplomystes viedmensis* MacDonagh) (Siluriformes: Diplomystidae).

Life cycle: IH1 *Heleobia hatcheri* (Pilsbry, 1911); IH2 *Galaxias maculatus*.

Localities: Limay River, Río Negro Province (type locality); Araucarian Region of the Andean Patagonia (see list of lakes and rivers in Ostrowski de Núñez *et al.*, 1999).

Site of infection: Intestine.

References: Szidat (1956b), Ostrowski de Núñez *et al.* (1999), Shimazu *et al.* (2000), Revenga *et al.* (2006a, b).

***Acanthostomum* Looss, 1899**

***Acanthostomum guerii* Szidat, 1954**

Material deposited: MACN-Pa 599 (type and new voucher material).

Hosts: *Rhamdia quelen* (Quoy & Gaimard) [= *Rhamdia sapo* (Valenciennes)] (type host), *Pimelodella laticeps* Eigenmann (Siluriformes: Heptapteridae), *Cyphocharax gilbert* (Quoy & Gaimard) [= *Pseudocurimata gilberti* (Quoy & Gaimard)] (Characiformes: Curimatidae).

Life cycle: IH1 *Heleobia parchappii* (Pilsbry) (Prosobranchia: Hydrobiidae); IH2 *Cnesterodon decemmaculatus* (Jenyns) (Cyprinodontiformes: Poeciliidae), *Odontesthes bonariensis* (Valenciennes) [= *Basilichthys bonariensis* (Valenciennes)] (Atheriniformes: Atherinopsidae), *Astyanax* sp., *Jenynsia multidentata* (Jenyns) [= *Jenynsia lineata* (Jenyns)], *Oligosarcus* sp. (= *Acestrorhamphus* sp.); FH *Rhamdia quelen*, *Pimelodella laticeps*.

Localities: Paraná River near Rosario City (type locality), Santa Fe Province; Chis-Chis and Chascomús Lagoon (Chascomús) and Cantera (quarry) Los Talas (Berisso), Buenos Aires Province.

Site of infection: Stomach (Lunaschi, 1986), anterior part of intestine.

References: Szidat (1954), Lunaschi (1986), Ostrowski de Núñez & Gil de Pertierra (1991), Gil de Pertierra & Ostrowski de Núñez (1995).

***Neoclodocystis* Manter & Pritchard, 1969**

***Neoclodocystis intestinalis* (Vaz, 1932)**

Material deposited: CHIOC, MACN-Pa.

Host: *Salminus brasiliensis* (type host, Brazil).

Life cycle: IH1 *Aylacostoma chloroticum* Hylton Scott; IH2 *Moenckhansia dichroua* (Kner), *Hyphessobrycon eques* (Steindachner) (natural hosts), *Poecilia reticulata*

Peters, *Cnesterodon decemmaculatus*, *Gymnocorymbus ternetzi* (Boulenger), *Prochilodus* sp. (experimental hosts); FH *Salminus brasiliensis*.

Localities: Tietê and Mogy-Guaçu rivers, São Paulo State, Brazil (type locality); Yacyretá Dam, Corrientes Province.

Site of infection: Pyloric caeca, intestine.

Reference: Quintana & Ostrowski de Núñez (2016).

Remarks: First record of the species and its life cycle in Argentina.

***Palaeocryptogonimus* Szidat, 1954**

***Palaeocryptogonimus claviformis* Szidat, 1954**

Material deposited: MACN-Pa (type material).

Hosts: *Rhinodoras dorbignyi* (type host).

Locality: La Plata River in front of Buenos Aires City (type locality).

Site of infection: Stomach, anterior part of intestine.

Reference: Szidat (1954).

***Parspiua* Pearse, 1920**

***Parspiua argentinensis* (Szidat, 1954)**

Proneochoasmus argentinensis Szidat, 1954

Material deposited: MACN-Pa (type and voucher material).

Hosts: *Pimelodus maculatus* [= *Pimelodus clarias* (Linnaeus)] (type host), *P. albicans*, *P. argenteus*, *Iheringichthys labrosus*, *Pimelodella gracilis*, *Parapimelodus valenciennis* (Lütken) (Siluriformes; Pimelodidae).

Localities: La Plata River in front of Buenos Aires City (type locality); Colastiné River (tributary of Paraná River), Santa Fe Province; Paraná-Guazú River, Entre Ríos Province.

Site of infection: Stomach, anterior, middle and posterior part of intestine.

References: Szidat (1954), Ostrowski de Núñez *et al.* (2011a).

Remarks: Ostrowski de Núñez *et al.* (2011a) redescribed and studied the tegument surface of the species.

***Parspiua carapo* Ostrowski de Núñez, Arredondo & Gil de Pertierra, 2011**

Material deposited: MACN-Pa (type material).

Host: *Gymnotus* sp. (type host) (Gymnotiformes: Gymnotidae) (see remarks).

Localities: Paraná-Guazú River, Entre Ríos Province (type locality); Colastiné River (tributary of Paraná River), Santa Fe Province.

Site of infection: Middle and posterior part of intestine.

Reference: Ostrowski de Núñez *et al.* (2011b).

Remarks: Ostrowski de Núñez *et al.* (2011b) studied the tegument surface of the species, which was compared with that of *Parspiua argentinensis*. Ostrowski de Núñez *et al.* (2011b) indicated the presence of *P. carapo* in *Gymnotus carapo*, but according to Froese & Pauly (2016) and Casciotta *et al.* (2013) this species is not present in continental waters of Argentina.

***Parspiua pimelodellae* Arredondo & Ostrowski de Núñez, 2013**

Material deposited: MACN-Pa (type material).

Host: *Pimelodella gracilis* (type host).

Locality: Paraná-Guazú River, Entre Ríos Province (type locality).

Site of infection: Anterior part of intestine.

Reference: Arredondo & Ostrowski de Núñez (2013).

***Parspiua virescens* Ostrowski de Núñez, Arredondo & Gil de Pertierra, 2011**

Material deposited: MACN-Pa (type material).

Host: *Eigenmannia virescens* (Valenciennes) (type host) (Gymnotiformes: Sternopygidae).

Locality: Colastiné River (tributary of Paraná River) (type locality), Santa Fe Province.

Site of infection: Pyloric caeca, anterior and middle part of intestine.

Reference: Ostrowski de Núñez *et al.* (2011b).

Remarks: Ostrowski de Núñez *et al.* (2011b) studied the tegument surface of the species, which was compared with that of *Parspiua argentinensis* and *P. carapo*.

***Pseudosellacotyla* Yamaguti, 1954**

***Pseudosellacotyla lutzi* (Freitas, 1941)**

Sellacotyle lutzi Freitas, 1941

Material deposited: CHIOC (type material), MACN-Pa.

Hosts: *Hoplias malabaricus* (Bloch) (type host, Brazil) (Characiformes: Erythrinidae).

Life cycle: IH1 *Aylacostoma chloroticum* Hylton Scott (Prosobranchia: Thiaridae); IH2 *Moenckhausia dichroua*, *Hyphessobrycon eques* (Characiformes: Characidae) (natural host); *Poecilia reticulata*, *Cnesterodon decemmaculatus* (Cyprinodontiformes: Poeciliidae), *Gymnocorymbus ternetzi* (experimental hosts) (Characiformes: Characidae).

Localities: Brazil (type locality); Middle Paraná River: Yacyretá Dam, Corrientes Province, and Heller Peninsula and Candelaria, Misiones Province.

Site of infection: Pyloric caeca and intestine.

References: Freitas (1941a), Quintana & Ostrowski de Núñez (2014).

Family Derogenidae Nicoll, 1910
***Deropegus* McCauley & Pratt, 1961**
***Deropegus patagonicus* (Szidat, 1956)**

Derogenes patagonicus Torres, 1995

Thometrema patagonica Lunaschi & Drago, 2000 (published in 2001)

Material deposited: IPCAS, MACN-Pa (type material), NSMT-PI.

Hosts: *Percichthys trucha* (type host), *P. collmapiensis*, *Salmo trutta*, *Salvelinus fontinalis*.

Localities: Pellegrini Lake and Limay River, Río Negro Province [type locality not assigned by Szidat (1956)]; Aluminé and Huechulafquén Lakes, Neuquén Province.

Site of infection: Stomach.

References: Szidat (1956b), Shimazu *et al.* (2000), Lunaschi & Drago, 2000 (published in 2001).

***Genarchella* Travassos, Artigas & Pereira, 1928**

Paravitellotrema Watson, 1976

Caballeroiella Lamothe-Argumedo, 1977

Graziatrema Nazir & Velásquez, 1977

Quadrupaludus Jiménez, Guajardo & Briseno, 1981

***Genarchella fragilis* Lunaschi, 1990**

Material deposited: MLP (type material).

Hosts: *Astyanax fasciatus* (Cuvier), *A. abramis* (Jenyns) (type host not assigned) (Characiformes: Characidae).

Locality: Doña Flora Stream (Ensenada), Buenos Aires Province (type locality).

Site of infection: Stomach.

Reference: Lunaschi (1990).

***Genarchella genarchella* (Travassos, Artigas & Pereira, 1928)**

Halipegus genarchella Travassos, Artigas & Pereira, 1928

Genarchella dubia Travassos, Artigas & Pereira, 1928

Material deposited: CHIOC (type material), MACN-Pa 600, 601, 602, 603 (new voucher material).

Hosts: *Oligosarcus* sp. (= *Acestrorhamphus* sp.) (type host, Brazil); *O. jenynsii* (Günther), *Charax stenopterus* (Cope) (= *Asiphonichthys stenopterus* Cope) (Characidae: Characidae), *Salminus brasiliensis*, *Leporinus friderici* (Bloch) (Characidae: Anostomidae); *Iheringichthys labrosus**, *Luciopimelodus pati**, *Pimelodus albicans*, *P. maculatus* (= *Pimelodus clarias* Linnaeus).

Localities: Emas Pirassununga, São Paulo State, Brazil (type locality); Middle Paraná River, El Dorado, Misiones Province; Colastiné River** (tributary of Paraná River), Santa Fe Province; Paraná-Guazú River**, Entre Ríos Province; Lujan River (Luján), Los Talas (Berisso), and Chascomús Lagoon (Chascomus), Buenos Aires Province.

Site of infection: Esophagus, stomach, intestine.

Life cycle: IH1 and IH2 *Heleobia australis* (d'Orbigny) (see Szidat, 1956); *H. parchappii* (see Martorelli, 1989).

References: Szidat (1956a), Martorelli (1989), Kohn *et al.* (1990), Arredondo (2013).

Remarks: New hosts and locality records. Szidat (1956a) mentioned *H. australis* as intermediate host, but this is a misidentification (see Martorelli, 1989). The progenetic metacercaria produces viable eggs, which are infective for the snail. The life cycle could be maintained without a vertebrate host for several years (Martorelli, 1989).

***Genarchella parva* Travassos, Artigas & Pereira, 1928**

Genarchella tropica (Manter, 1936) Szidat 1954 *nec* *Derogenes tropicus* Manter, 1936

Genarchella szidati (Yamaguti, 1971).

For more synonyms see Lunaschi (1990) and Kohn *et al.* (2007).

Material deposited: CHIOC (type material), MACN-Pa 604, 605 (new voucher material).

Hosts: *Oligosarcus* sp. (= *Acestrorhamphus* sp.) (type host, Brazil), *Oligosarcus jenynsii*, *O. hepsetus* (Cuvier), *Charax gibbosus* (Linnaeus) (= *Cynopotamus gibbosus* Valenciennes) (Characidae: Characidae), *Salminus brasiliensis*, *Triportheus paranensis*, *Astyanax* sp., *A. bimaculatus* [= *Poeciloristhys bimaculatus* (Linnaeus)], *A. eigenmanniorum* (Cope), *A. fasciatus*, *Cheirodon interruptus* Jenyns, *Hy-*

phessobrycon meridionalis Ringuelet, Miquelarena & Menni, *Jenynsia multidentata* [= *J. lineata* (Jenyns)] (Cyprinodontiformes: Anablepidae), *Ageneiosus militaris**, *Auchenipterus nigripinnis*, *A. osteomystax* (= *A. nuchalis*), *Leporinus obtusidens*, *Loricariichthys anus* (Valenciennes) (= *Loricaria anus* Valenciennes) (Siluriformes: Loricariidae), *Luciopimelodus pati*, *Pimelodus albicans*, *P. argenteus*, *P. maculatus*, *P. ornatus* Kner, *Pseudoplatystoma corruscans* (Spix & Agassiz)*, *Pimelodella gracilis*, *Pimelodella mucosa* Eigenmann & Ward (= *Pimelodella howesi* Fowler), *Rhamdia quelen* (= *R. sapo*).

Localities: Emas Pirassununga, São Paulo State, Brazil (type locality); Paraná River (Puerto Italia), Corrientes City, Corrientes Province; Colastiné River** (tributary of Paraná River), Santa Fe Province; Saladita Lagoon (Avellaneda), Cantera (quarry) Aprilito (Ensenada), Doña Flora Stream (Ensenada), Miguelín Stream (Ensenada), Cantera (quarry) Los Talas (Berisso), Chascomús and Chis-Chis Lagoons (Chascomús) and Luján River (Luján), Buenos Aires Province; La Plata River in front of Buenos Aires City.

Site of infection: Stomach.

References: Szidat (1954), Hamann (1989), Lunaschi (1990), Gil de Perterra & Ostrowski de Núñez (1995), Drago (1997), Arredondo (2013).

Remarks: New hosts and locality records. Referred to as *Genarchella szidati* Yamaguti, 1971 by Hamann (1989). Hamann (1989) indicated that the records of *Genarchella parva* in *Auchenipterus nuchalis*, *Jenynsia lineata* and *Pimelodella howesi*, in Argentina probably correspond to *A. osteomystax*, *J. multidentata* and *P. mucosa*, respectively (see Liotta, 2005; Aguilera & Azpelicueta, 2015; Froese & Pauly, 2016).

Thometrema Amato, 1968

Thometrema bonariensis Lunaschi, 1988

Material deposited: MLP (type and voucher material).

Host: *Australoheros facetus* (= *Cichlasoma facetum*) (type host); *Odontesthes bonariensis* (Atheriniformes: Atherinopsidae).

Locality: Chascomús Lagoon (Chascomús) (type locality), and Salada Grande Lagoon (General Lavalle), Buenos Aires Province.

Site of infection: Stomach, intestine.

References: Lunaschi (1988a), Drago (2004, 2012).

Thometrema magnifica (Szidat, 1954)

Gonocercella magnifica Szidat, 1954

Thometrema portoalegrensis Amato, 1968

Material deposited: MACN-Pa 606 (type material and new voucher material), MLP.

Hosts: *Hypostomus plecostomus* (Linnaeus) [= *Plecotomus plecostomus* (Linnaeus)], *Hypostomus comuersoni* Valenciennes [= *Plecotomus coumersoni* (Valenciennes)] (type host not assigned), (Siluriformes: Loricariidae).

Localities: Uruguay River in front of Santo Tomé, Corrientes Province and La Plata River in front of Buenos Aires City (type locality not assigned); Paraná-Guazú River**, Entre Ríos Province; Canal Yrigoyen, Isla Talavera, Buenos Aires Province.

Site of infection: Stomach, swim bladder.

References: Szidat (1954), Gibson & Bray (1979), Kohn *et al.* (1983), Lunaschi & Sutton (1995), Arredondo (2013).

Remarks: New host and locality records. Szidat (1954) indicated the presence of *Thometrema magnifica* in *Plecotomus plecostomus*, but according to Froese & Pauly (2016) and Almirón *et al.* (2015) this species is not present in continental waters of Argentina. Probably, due to similarity among them, the record of *Hypostomus plecostomus* by Szidat (1954) corresponds to *Pterygoplichthys anisitsi* which inhabits the Paraná River basin.

Thometrema overstreeti (Brooks, Mayes & Thorson, 1979)

Paravitellotrema overstreeti Brooks, Mayes & Thorson, 1979

Thometrema rioplatense Lunaschi, 1988

For more synonyms see Kohn *et al.* (2007)

Material deposited: MACN-Pa 607, 608 (new voucher material), MLP, USNM (type material).

Host: *Potamotrygon magdalenae* (Dumeril) (Myliobatiformes: Potamotrygonidae) (type host); *Astyanax fasciatus*, *A. paraguayensis* (Fowler), *Leporinus obsutidens*, *Oligosarcus jenynsii*, *Salminus brasiliensis*, *Ageneiosus inermis*, *Auchenipterus nigripinnis*, *Luciopimelodus pati*, *Pimelodus albicans*, *P. maculatus*, *Pseudoplatystoma corruscans*, *P. reticulatum* Eigenmann & Eigenmann, *Sorubim lima* Bloch & Schneider, *Rhamdia quelen*, *Zungaro jahu* (Ihering) [= *Paulicea huetkeni* (Steindachner)].

Localities: Magdalena River in northern Colombia (type locality); Middle Paraná River, Puerto Italia, Corrientes Province; Colastiné River** (tributary of Paraná River), Santa Fe Province; Paraná-Guazú River**, Entre Ríos Province; Chis-Chis Lagoon (Chascomús), Doña Flora Stream (Ensenada), Miguelín Stream (Ensenada) and La Plata River, Buenos Aires Province.

Site of infection: Stomach.

References: Brooks *et al.* (1979), Hamann (1986, 1989), Lunaschi (1988a), Gil de Pertierra & Ostrowski de Núñez (1995), Arredondo (2013).

Remarks: New localities records. Referred to as *Genarchella genarchella* by Hamann (1986, 1989).

Family Faustulidae Poche, 1926

***Bacciger* Nicoll, 1914**

***Bacciger astyanactis* Lunaschi, 1998**

Material deposited: MLP (type material).

Host: *Astyanax fasciatus* (type host).

Locality: La Plata River (type locality) and Bagliardi Beach (Ensenada), Buenos Aires Province.

Site of infection: Rectum.

Reference: Lunaschi (1988c).

***Bacciger delvalleensis* Lunaschi, 2001**

Material deposited: MLP (type material).

Host: *Astyanax eigenmanniorum* (type host).

Locality: Cuña-pirú Stream, Aristóbulo del Valle, Misiones Province (type locality).

Site of infection: Rectum.

Reference: Lunaschi (2001).

Family Glythelminthidae Cheng, 1959

***Glythelminius* Stafford, 1905**

***Glythelminius pseudium* (Mañé-Garzón & Holcman-Spector, 1967)**

Margeana pseudium Mañé-Garzón & Holcman-Spector, 1967

Material deposited: MLP.

Host: *Pseudis minuta* (Günther) (= *Pseudis mantidactylus* Boulenger) (type host) (Anura: Hylidae); *Corydoras paleatus* (Jenyns) (Siluriformes: Callichthyidae).

Locality: Bañados de la Coronilla, Departamento de Rocha and Bañado Tropa Vieja, Canelones, Uruguay (type locality); Villoldo Stream, Buenos Aires Province.

Site of infection: Intestine.

Reference: Lunaschi (1991).

Remarks: This species parasitizes amphibians and is considered an accidental infection in the fish by Lunaschi (1991).

Family Gorgoderidae Loos, 1901

***Phyllodistomum* Braun, 1899**

***Phyllodistomum mugilis* Knoff & Amato, 1992**

Material deposited: CHIOC (type material), MLP.

Hosts: *Mugil liza* Valenciennes (= *Mugil platanus* Günther) (type host, Brazil).

Locality: Guanabara Bay, Rio de Janeiro State, Brazil (type locality); Ajo River, Samborombón Bay, Buenos Aires Province.

Site of infection: Urinary bladder.

References: Montes *et al.* (2012), Montes (2013), Montes & Martorelli (2015).

***Phyllodistomum spatula* Odhner, 1902**

Material deposited: Information about type material not provided by Odhner (1902), MLP.

Host: *Bagrus bayad* (Forsskål) [= *B. bayad* (Forsskål)] and *B. docuak* (Forsskål) [= *B. docmac* (Forsskål)] (Siluriformes: Bragridae) (type host not assigned, Sudan); *Pimelodella laticeps*, *Rhamdia quelen*.

Life cycle: IH1: *Palaemonetes argentinus* Nobili; FH: *P. laciceps*, *R. quelen* (natural hosts).

Localities: Nile River, Omdurman, Sudan (type locality); Chascomús Lagoon (Chascomús), Buenos Aires Province.

Site of infection: Urinary bladder.

Reference: Lunaschi & Martorelli (1990).

Remarks: The existence of this African species in South America has to be carefully reviewed. The specimens studied by Lunaschi & Martorelli (1990) probably could belong to *Phyllodistomum rhamdiae* Amato & Amato, 1993 described from the urinary bladder of *Rhamdia quelen* in Brazil (see Amato & Amato, 1993).

Family Haploporidae Nicoll, 1914

***Chalciuotrema* Freitas, 1947**

***Chalciuotrema plateuse* (Lunaschi, 1984)**

Saccocoelioides platensis Lunaschi, 1984

Material deposited: MLP (type material).

Host: *Cyphocharax platanus* (Günther) [= *Curimatorbis platanus* (Günther)] (type host) (Characiformes: Curimatidae).

Locality: Boca Cerrada (Ensenada), Buenos Aires Province (type locality).

Site of infection: Intestine.

References: Lunaschi (1984b), Overstreet & Curran (2005).

***Chalcinotrema salobrensis* Freitas, 1947**

Material deposited: CHIOC (type material), MACN-Pa.

Hosts: *Triportheus paranensis* (= *Chalcinus paranensis*) (type host, Brazil); *Piaractus mesopotamicus*.

Localities: Miranda River (tributary of Paraguay River), Salobra, Mato Grosso State, Brazil (type locality); Middle Paraná River, Corrientes Province.

Site of infection: Anterior and middle part of intestine.

References: Freitas (1947), Hamann (1983).

***Forticulcita* Overstreet, 1982**

***Forticulcita platana* Andres, Curran, Fayton, Pulis & Overstreet, 2015**

Material deposited: MACN-Pa (type material), USNM (type material).

Host: *Mugil liza* (type host) (Mugiliformes: Mugilidae).

Localities: La Plata River, Punta Lara, (type locality); Salado River, Cerro de la Gloria, Buenos Aires Province.

Site of infection: Intestine.

Reference: Andres *et al.* (2015).

***Megacoelium* Szidat, 1954**

***Megacoelium plecostomi* Szidat, 1954**

Material deposited: MACN-Pa 609 (type material and voucher material).

Host: *Hypostomus plecostomus* (= *Plecostomus plecostomus*) (type host); *Hypostomus commersoni**.

Localities: La Plata River in front to Buenos Aires City, Uruguay River in front of Santo Tomé City, Corrientes Province [type locality not assigned by Szidat (1954)]; Paraná-Guazú River**, Entre Ríos Province.

Site of infection: Stomach, anterior part of intestine.

References: Szidat (1954), Arredondo (2013).

Remarks: New host and locality record. Szidat (1954) indicated the presence of *Megacoelium plecostomi* in *Plecostomus plecostomus*, but according to Froese & Pauly (2016) and Almirón *et al.* (2015) this species is not present in continental waters of Argentina. Probably, due to similarity among them, the record of *Hypostomus plecostomus* by Szidat (1954) corresponds to *Pterygoplichthys anisitsi* which inhabits the Paraná River basin.

***Saccocoelioides* Szidat, 1954**

Lecithobothrioides Thatcher & Dossman, 1974

***Saccocoelioides antonioni* Lunaschi, 1984**

Material deposited: MLP (type material).

Host: *Cyphocharax platamus* (type host).

Locality: Boca Cerrada (Ensenada), Buenos Aires Province (type locality).

Site of infection: Pyloric caeca.

Reference: Lunaschi (1984b).

***Saccocoelioides bacilliformis* Szidat, 1973**

Material deposited: MACN-Pa (type material).

Host: *Astyanax bipunctatus* (non valid species) probably *A. cf. bimaculatus* (Linnaeus) (see Lunaschi, 2002).

Localities: Reconquista River, Buenos Aires Province (type locality).

Site of infection: Pyloric ceca.

Reference: Szidat, 1973.

Remarks: Lunaschi (2002) considered *Saccocoelioides bacilliformis* junior synonym of *Saccocoelioides octavus* Szidat, 1970. However, Kohn *et al.* (2007) considered this species valid (see Discussion).

***Saccocoelioides carolae* Lunaschi, 1984**

Material deposited: MLP (type material).

Host: *Australoheros facetus* (= *Cichlasoma facetum* Jenyns) (type host).

Life cycle: IH1 *Heleobia parchappii*, unencysted metacercaria, without tail, free in water; FH *A. facetus*.

Localities: Los Talas (Berisso), Buenos Aires Province.

Site of infection: Intestine.

References: Lunaschi (1984b), Martorelli (1986).

***Saccocoelioides elongatus* Szidat, 1954**

Material deposited: MACN-Pa (type material).

Host: *Prochilodus lineatus* (Valenciennes) (= *Prochilodus platensis* Holmberg) (type host).

Localities: La Plata River, in front of Buenos Aires City (type locality), Middle Paraná River, Corrientes Province.

Site of infection: Intestine.

References: Szidat (1954), Hamann (1982c).

Remarks: Lunaschi (1996) considered *Saccocoelioides elongatus* junior synonym of *Saccocoelioides nanii* Szidat, 1954. However, Kohn *et al.* (2007) considered this species valid (see Discussion).

***Saccocoelioides magniovatus* Szidat, 1954**

Material deposited: MACN-Pa (type material).

Host: *Leporinus obtusidens* (type host).

Localities: Luján River, Buenos Aires Province (type locality).

Site of infection: Intestine.

Reference: Szidat (1954).

Remarks: Lunaschi (1996) considered *Saccocoelioides magniovatus* junior synonym of *S. nanii* Szidat, 1954. However, Kohn *et al.* (2007) considered this species valid (see Discussion).

***Saccocoelioides magnus* Szidat, 1954**

Material deposited: MACN-Pa (type material).

Host: *Cyphocharax platanus* [= *Crimata platana* (Günther)] (type host).

Localities: Middle Paraná River, in front of Rosario City, Santa Fe Province (type locality).

Site of infection: Intestine.

Reference: Szidat (1954).

***Saccocoelioides nanii* Szidat, 1954**

Material deposited: MACN-Pa (type material), MLP.

Host: *Prochilodus lineatus*, *Hypostomus commersoni*, *Hyphessobrycon meridionalis*.

Localities: Middle Paraná River, in front of Rosario City, Santa Fe Province (type locality); Irigoyen Canal (Talavera Island) and Saladita Lagoon (Avellaneda), Buenos Aires Province.

Site of infection: Intestine.

References: Szidat (1954), Lunaschi (1996), Drago (1997).

Remarks: Lunaschi (1996) considered *S. elongatus* and *S. magniovatus* junior synonyms of *S. nanii* Szidat, 1954. However, Kohn *et al.* (2007) considered these species valid (see Discussion).

***Saccocoelioides octavus* Szidat, 1970**

Material deposited: MACN-Pa (type material).

Hosts: *Astyanax fasciatus* (type host).

Life cycle: H11 *Heleobia parchappii*, encysted metacercaria with attached tail free swimming in water.

Localities: Artificial small stream connected with Chascomús Lagoon (Chascomús), Buenos Aires Province.

Site of infection: Pyloric caeca, intestine.

References: Szidat (1970a), Lunaschi (2002).

***Saccocoelioides quintus* Thatcher, 1978**

Material deposited: MACN-Pa (type material).

Host: *Loricariichthys anns* (Valenciennes) (= *Loricaria anns* Valenciennes) (type host) (Siluriformes: Loricariidae).

Localities: Middle Paraná River, in front of Rosario City, Santa Fe Province (type locality); Paraná River, Corrientes Province.

Site of infection: Intestine.

References: Szidat (1954), Thatcher (1978).

Remarks: Referred to as *Saccocoelioides* sp. 5 by Szidat (1954).

***Saccocoelioides szidati* Travassos, Freitas & Kohn, 1969**

Material deposited: MACN-Pa (type material).

Host: *Schizodon fasciatus* Spix & Agassiz (Characiformes: Anostomidae) (type host); *L. obtusidens*.

Localities: Middle Paraná River, in front of Rosario City, Santa Fe Province (type locality); Middle Paraná River, Corrientes Province.

Site of infection: Intestine.

References: Szidat (1954), Travassos *et al.* (1969), Hamann (1983).

Remarks: Referred to as *Saccocoelioides* sp. 6 by Szidat (1954).

***Xiha* Andres, Curran, Fayton, Pulis & Overstreet, 2005**

***Xiha fastigata* (Thatcher & Sparks, 1958)**

Dicrogaster fastigatus Thatcher & Sparks, 1958

Material deposited: MLP, USNM (type material).

Host: *Mugil cephalus* Linnaeus (type host, USA), *Mugil liza* (Mugiliformes: Mugilidae).

Life cycle: IH1 *Heleobia conexa* (Gaillard), cysts of metacercaria free in water.

Localities: Grand Isle (Louisiana), Gulf of México, USA (type locality); Salado River relief canal and Ajo River, Samborombón Bay, Mar Chiquita Lagoon (Mar Chiquita), Buenos Aires Province.

Site of infection: Intestine.

References: Alarcos & Etchegoin (2010), Montes *et al.* (2012), Montes (2013), Lado *et al.* (2013), Montes & Martorelli (2015), Andres *et al.* (2015).

Remarks: Alarcos & Etchegoin (2010), Montes (2012), Montes *et al.* (2012), and Montes & Martorelli (2015) reported *Dicrogaster fastigatus* in Argentina. Recently, Andres *et al.* (2015) transferred the specimens described as *Dicrogaster fastigatus* by Thatcher & Sparks (1958) to a new genus, as *Xiha fastigata*. Even though Andres *et al.* (2015) did not comment on the Argentinian records for *Dicrogaster fastigatus*, these specimens have a spined hermaphroditic duct as it is present in *Xiha* (Montes, 2013).

Family Haplospilichnidae Poche, 1926

***Hymenocotta* Manter, 1961**

***Hymenocotta manteri* Overstreet, 1969**

Material deposited: MLP, USNM (type material).

Hosts: *Mugil cephalus* Linnaeus (type host, USA), *M. liza*.

Locality: Biscayne Bay, Florida, USA (type locality); Salado River relief canal and Ajo River, Samborombón Bay, Buenos Aires Province.

Site of infection: Intestine.

References: Montes *et al.* (2012), Montes (2013), Montes & Martorelli (2015).

Family Hemiuridae Loos, 1899

***Dinurus* Looss, 1907**

***Dinurus breviductus* Looss, 1907**

Dinurus barbatus (Cohn, 1902)

Material deposited: MACN-Pa.

Hosts: *Rannogaster melanostoma* (Eigenmann) [= *Clupea melanostoma* (Eigenmann)] (Clupeiformes: Clupeidae) (type host); *Rhaphiodon vulpinus* Spix & Agassiz (Characiformes: Cynodontidae).

Locality: La Plata River, Buenos Aires Province.

Site of infection: Free in coelomic cavity.

Reference: Szidat *et al.* (1950).

Remarks: Szidat *et al.* (1950) found numerous eggs in the worms inhabiting the coelomic cavity.

***Stomachicola* Yamaguti, 1934**

***Stomachicola lycengraulidis* Tanzola & Seguel, 2012**

Material deposited: MLP (type material), MACN-Pa 610/1–2.

Hosts: *Lycengraulis grossidens* (Agassiz) (Clupeiformes: Engraulidae) (type host).

Locality: Bahía Blanca estuary (type locality) and Paraná River, Buenos Aires Province; Paraná-Guazú River**, Entre Ríos Province.

Site of infection: Stomach.

Reference: Tanzola & Seguel (2012), Arredondo (2013).

Remarks: New locality record. Tanzola & Seguel (2012) also recorded this species in the marine fish *Conger orbignianus* Valenciennes.

Lecithasteridae Odhner, 1905

***Lecithaster* Lühe, 1901**

***Lecithaster confusus* Odhner, 1905**

Material deposited: NRM (type material), MLP.

Host: *Alosa agone* (Scopoli) [= *A. finta* (Cuvier)] and *Clupea harengus* Linnaeus (Clupeiformes: Clupeidae) (type host not assigned); *Jenynsia multidentata*.

Locality: Mediterranean and North Sea (type locality not assigned, Europe); Salado River relief canal, Samborombón Bay, Buenos Aires Province.

Site of infection: Intestine.

Reference: Montes (2013).

Remarks: Montes (2013) recorded the presence of this Mediterranean and North Sea species in South America. These specimens have to be carefully reviewed, they probably could belong to *Lecithaster intermedius* Szidat, 1954 (see below).

***Lecithaster intermedius* Szidat, 1954**

Material deposited: MACN-Pa (type material).

Host: *Rannogaster melanostoma* (type host).

Locality: La Plata River in front of Buenos Aires City (type locality).

Site of infection: Intestine.

Reference: Szidat (1954).

Family Microscaphidiidae Loos, 1900

***Curumai* Travassos, 1961**

***Curumai curumai* Travassos, 1961**

Material deposited: CHIOC (type material), MACN-Pa 613 (new voucher material).

Hosts: *Myleus* sp. (Characiformes: Serrasalminae) (type host, Brazil); *Piaractus mesopotamicus*; *Pterodoras granulosus**.

Localities: Amazon River (Pará State), Brazil (type locality); Middle Paraná River, Corrientes Province; Colastiné River ** (tributary of the Paraná River), Santa Fe Province.

Site of infection: Intestine.

References: Hamann (1982a), Arredondo (2013).

Remarks: New host and locality record.

Family Plagiorchiidae (Lühe, 1901)

Kalipharynx Boeger & Thatcher, 1983

Kalipharynx pirauboe Boeger & Thatcher, 1983

Material deposited: IOC (type material), MLP.

Host: *Lepidosiren paradoxa* Fitzinger (Dipnoi: Lepidosirenidae) (type host, Brazil).

Localities: Amazon River, Manaus City, Brazil (type locality); Paraná River, Resistencia City, Chaco Province.

Site of infection: Anterior part of intestine.

References: Boeger & Thatcher (1983), Lunaschi (1994).

Remarks: *Kalipharynx* Boeger & Thatcher, 1983 is considered as genus *incertae sedis* by Pojmańska *et al.* (2008).

Family Zonocotyliidae Yamaguti, 1963

Zonocotyle Travassos, 1948

Zonocotylodes Padilha, 1978

Zonocotyle bicaecata Travassos, 1948

Material deposited: CHIOC (type material), MLP.

Host: *Steindachnerina elegans* (Steindachner) [= *Curimata elegans* (Steindachner)] (type host, Brazil), *Cyphocharax gilbert* (Quoy & Gaimard) [= *Pseudocurimata gilberti* (Quoy & Gaimard)], *Cyphocharax platanus* (Günther) [= *Curimatorbis platanus* (Günther)], *Steindachnerina brevipinna* (Eigenmann & Eigenmann) [= *Pseudocurimata nitens* (Holmberg)] (Characiformes: Curimatidae).

Localities: Mogi-Guaçu River, (Emas, Pirassununga), São Paulo State, Brazil (type locality); Los Talas (Berisso), Buenos Aires Province.

Site of infection: Intestine.

References: Travassos (1947), Lunaschi (1988b).

Family Zoogonidae Odhner, 1911

Porangatus Fernandes, Malta & Morias, 2013

Porangatus ceteyus Fernandes, Malta & Morias, 2013

Material deposited: CHIOC (type material), MACN-Pa 615/1–2 (new voucher material).

Host: *Hoplosternum littorale* (Siluriformes: Callichthyidae) (type host).

Localities: Lake Catalão, Amazonas State, Brazil (type locality); Paraná-Guazú River**, Entre Ríos Province.

Site of infection: Middle and posterior part of intestine.

References: Arredondo (2013), Fernandes *et al.* (2013).

Remarks: First citation of this species in Argentina.

Steganoderma Stafford, 1904

Steganoderma macrophallus Szidat & Nani, 1951

Material deposited: MACN-Pa (type material).

Host: *Basilichthys microlepidotus* (Jenyns) (= *Basilichthys microlepidota* Girard) (Atheriniformes: Atherinopsidae) (type host).

Localities: Limay River (Plottier), Neuquén Province (type locality); Quequén River (Buenos Aires Province).

Site of infection: Intestine.

Reference: Szidat & Nani (1951).

Steganoderma szidati Viozzi, Flores & Ostrowski de Núñez, 2000

Material deposited: MAC-Pa (type material), UNC (type material).

Host: *Galaxias maculatus* (Jenyns) (type host), *Galaxias platei* Steindachner, *Aplochiton zebra* Jenyns (Osmeriformes: Galaxiidae).

Localities: Gutiérrez Lake, Rio Negro Province (type locality); Glacial lakes of Andean Patagonia; Moreno and Nahuel Huapi Lakes, Rio Negro Province; Epuyén and Cholila Lakes, Chubut Province.

Site of infection: Posterior part of intestine.

References: Viozzi *et al.* (2000, 2009), Revenga *et al.* (2005), Fernández *et al.* (2012, 2015a, b).

Steganoderma valchetensis Etchegoin, Cremonte & Escalante, 2002

Material deposited: BMNH (type material), MLP (type material).

Host: *Gymnocharacinus bergii* Steindachner (Characiformes: Characidae) (type host).

- Dipnoi
Fam. Lepidosirenidae
Lepidosiren paradoxa
Kalipharynx piramboae
- Gymnotiformes
Fam. Gymnotidae
Gymnotus sp.
Parspina carapo
Fam. Rhamphichthyidae
Rhamphichthys rostratus
Auriculostoma platense
Fam. Sternopygidae
Eigenmannia virescens
Parspina virescens
- Mugiliformes
Fam. Mugilidae
Mugil liza
Forticulcita platana
Hymenocotta manteri
Phyllodistomum mugilis
Xiha fastigata
- Osmeriformes
Fam. Galaxiidae
Aplochiton zebra
Steganoderma szidati
Galaxias maculatus
Acanthostomoides apophalliformis
Allocreadium pichi
Steganoderma szidati
G. platei
Steganoderma szidati
- Perciformes
Fam. Cichlidae
Australoheros facetus
Lobatostoma jungwirthi
Thometrema bonariensis
Saccocoelioides carolae
Cichlasoma dimerus
Crassicutis cichlasomae
Crenicichla lepidota
Crassicutis cichlasomae
Gymnogeophagus australis
Homalometron pseudopallidum
Fam. Percichthyidae
Percichthys colhuapiensis
Acanthostomoides apophalliformis
Allocreadium patagonicum
Deropegus patagonicus
P. trucha
Acanthostomoides apophalliformis
Allocreadium patagonicum
Deropegus patagonicus
Homalometron papilliferum
Posterotestes unelen
Fam. Sciaenidae
Pachyurus bonariensis
Auriculostoma macrorchis
- Pleuronectiformes
Fam. Achiridae
Catathyridium jenynsii
Prosorhynchoides rioplatensis
- Salmoniformes
Fam. Salmonidae
Onchorhynchus mikiss
Acanthostomoides apophalliformis
Salmo trutta
Acanthostomoides apophalliformis
Deropegus patagonicus
Salvelinus fontinalis
Deropegus patagonicus
- Siluriformes
Fam. Auchenipteridae
Ageniosus inermis
Auriculostoma macrorchis
Microrchis oligovitellinum
Thometrema overstreeti
A. militaris
Auriculostoma macrorchis
Genarchella parva
Microrchis oligovitellinum
Auchenipterus nigripinnis
Auriculostoma macrorchis
Genarchella parva
Thometrema overstreeti
A. osteomystax
Auriculostoma macrorchis
Genarchella parva
Trachelyopterus galeatus
Creptotrema creptotrema
Dadaytremoides parauchenipteri
T. striatulus
Creptotrema creptotrema
Microrchis oligovitellinum
Fam. Callichthyidae
Corydoras paleatus
Glyptelmis pseudium
Hoplosternum littorale
Magnivitellinum corvitellinum
Plethniella coelomicola
Porangatus ceteyus
Fam. Diplomystidae
Oliveichthys viednensis
Acanthostomoides apophalliformis
Fam. Doradidae
Pterodoras granulosus
Curumai curumai
Dadaytrema gracilis
D. oxycephala
Microrchis oligovitellinum
Travassosinia dilatata
Rhinodoras dorbignyi
Auriculostoma macrorchis
A. platense
Palaeocryptogonimus claviformis
Fam. Heptapteridae
Pimelodella gracilis
Dadaytrema gracilis
Genarchella parva
Parspina argentinensis
P. pimelodellae
P. laticeps
Acanthostomum gnerii
Phyllodistomum spatula
P. mucosa
Genarchella parva
Rhandia quelen
Acanthostomum gnerii
Genarchella parva
Phyllodistomum spatula

Thometrema overstreeti
 Fam. Loricariidae
Hypostomus commersoni
 Crassicutis intermedius
 Megacoelium plecostomi
 Thometrema magnifica
 Saccocoelioides nanii
*Hypostomus plecostomus**
 Megacoelium plecostomi
 Thometrema magnifica
Loricariichthys anus
 Genarchella parva
 Saccocoelioides quintus
Paraloricaria vetula
 Procaudotestis uruguayensis
 Fam. Pimelodidae
Iheringichthys labrosus
 Auriculostoma platense
 Genarchella genarchella
 Parspina argentinensis
 Plethniella coelomicola
Luciopimelodus pati
 Auriculostoma macrorchis
 Creptotrema pati
 Genarchella genarchella
 G. parva
 Microrchis oligovitellinum
 Prosthenlystera obesa
 Thometrema overstreeti
Parapimelodus valenciennis
 Parspina argentinensis
Pimelodus albicans
 Auriculostoma platense
 Genarchella genarchella
 G. parva
 Parspina argentinensis
 Plethniella coelomicola
 Prosthenlystera obesa
 Thometrema overstreeti
P. argenteus
 Auriculostoma platense
 Genarchella parva
 Parspina argentinensis
P. maculatus
 Auriculostoma platense
 Genarchella genarchella
 G. parva
 Parspina argentinensis
 Plethniella coelomicola
 Thometrema overstreeti
P. ornatus
 Genarchella parva
Pseudoplatystoma corruscans
 Genarchella parva
 Plethniella coelomicola
 Thometrema overstreeti
P. reticulatum
 Thometrema overstreeti
Sorubim lima
 Magnivitellinum simplex
 Thometrema overstreeti
Zungaro jahu
 Thometrema overstreeti

DISCUSSION

This checklist includes 77 species of adult trematodes (Aspidogastrea and Digenea) belonging to 45 genera and 21 families. The highest species richness was recorded for the family Haploporidae with 15 species, followed by Allocreadiidae and Cryptogonimidae, with nine species each. The number of species for the remaining 18 families ranges between one and seven species.

In regard to digeneans from Argentina, five new species were reported (*Forticulcita platana*, *Parspina carapo*, *P. pimelodellae* and *P. virescens* and *Stomachicola lycengranlidis*), and 9 were cited for the first time in the country (*Crassicutis cichlasomae*, *Hymenocotta manteri*, *Lecithaster confusus*, *Magnivitellinum corvitellinum*, *Neocladocystis intestinalis*, *Porangatus ceteyns*, *Phylodistomum mugilis*, *Pseudosellacotyla lutzii* and *Xiha fastigata*) between 2007 and 2016 (Kohn *et al.*, 2007, Ostrowski de Núñez *et al.*, 2011; Montes *et al.*, 2012; Tanzola & Seguel, 2012; Arredondo, 2013; Arredondo & Ostrowski de Núñez, 2013; Montes, 2013; Quintana & Ostrowski de Núñez, 2014; Andres *et al.*, 2015; Montes & Martorelli, 2015; Quintana & Ostrowski de Núñez, 2016). Moreover, new hosts were found for 17 species (*Auriculostoma macrorchis*, *A. platense*, *Creptotrema creptotrema*, *Crassicutis cichlasomae*, *Curumai curumai*, *Dadaytrema gracilis*, *Genarchella genarchella*, *G. parva*, *Hymenocotta manteri*, *Lecithaster confusus*, *Magnivitellinum simplex*, *Megacoelium plecostomi*, *Microrchis oligovitellinum*, *Parspina argentinensis*, *Plethniella coelomicola*, *Prosthenlystera obesa*, and *Travassosinia dilatata*). On the other hand, 28 digenean species have been recorded in new localities of Argentina (including new host records plus *Crassicutis intermedius*, *Dadaytrema oxycephala*, *Magnivitellinum corvitellinum*, *Neocladocystis intestinalis*, *Phylodistomum mugilis*, *Porangatus ceteyns*, *Pseudosellacotyla lutzii*, *Stomachicola lycengranlidis*, *Thometrema magnifica*, *T. overstreeti* and *Xiha fastigata*).

A final comment should be made on some trematode species: 1) The specimen of *Steganoderma oviformis* Szidat, 1962 reported from Argentina by Kohn *et al.* (2007) had actually been collected in Valdivia, Chile (see Fernández *et al.*, 2012); 2) there is controversy about the validity of some *Saccocoelioides* species described by Szidat (see Kohn, 1985; Lunaschi, 1996, 2002; Kohn *et al.*, 2007) because the type material of these species (deposited at the MACN) is poorly fixed and improperly stained, highlighting the need to clarify their taxonomic status by the examination of new material from type hosts and localities; 3) *Crassicutis cichlasomae* has a wide geographic distribution, as it parasitizes 25 species of cichlids in Mexico and other hosts in Central America (Nicaragua, Costa Rica and Cuba) and South America (Brazil) (Razo-Mendivil *et al.*, 2013). Recent genetic studies by Razo-Mendivil *et al.* (2010, 2013) revealed that *C. cichlasomae* represents a complex of cryptic species, requiring a thorough morphological characterization for

consistent species identification. Razo-Mendivil *et al.* (2013) suggest that *C. cichlasomae* specimens from Cuba and Brazil belong to a new species, and a similar line of reasoning may apply to the Argentinean specimens. Molecular studies of South American trematodes would help resolve some of these issues.

In the present checklist 34, 31, and 11 species of digeneans have been recorded in 26, 30 and seven species of Characiformes, Siluriformes and Perciformes, respectively. These orders not only show the highest species richness of freshwater fishes, but also harbour the highest species richness of digeneans in South America, including Argentina. The high diversity of trematodes reported in Characiformes and Siluriformes is probably due to the utmost sampling effort, as they included species of great commercial value, which makes them readily available for parasitologists. Future trematode studies might also include fish hosts used as baits, such as species of the families Characidae (Characiformes) locally called “mojaras”, Cichlidae (Perciformes) and all the families of Gymnotiformes (knifefish), which have been scarcely studied. Indeed, recent parasitological surveys of Gymnotiformes revealed the presence of two new species of the genus *Paraspina*. This highlights the importance of considering fishes of minor commercial value for the discovery of new trematodes.

Few years ago, Reis *et al.* (2003) listed 4475 valid fish species from South and Central America and assumed that about 1550 remain to be described. Recently, Reis (2013) added new records to the list of Neotropical fishes and estimated a total of 8000 fish species in the region. South America possesses two of the major hydrological basins of the world, namely the Amazon River and the Paraná-La Plata River basins, followed by the Uruguay River, which has been scarcely studied from a parasitological point of view. According to Choudhury *et al.* (2016), less than 5% of the highly diverse South American ichthyofauna has been examined for parasites, suggesting that the biodiversity of freshwater fish hosts and their adult trematodes in South America is underestimated.

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A new *Paramaronius* species from Argentina (Coleoptera: Cantharidae)

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Abstract: The new species *Paramaronius unituberculatus* sp. nov. from Salta province, northern Argentina, is described and illustrated. An updated identification key including also the new species is provided.

Keywords: Chauliognathinae - description - key - neotropical - taxonomy.

INTRODUCTION

Paramaronius Wittmer, 1963 is readily recognized by the remarkable sculptural modifications and pubescence on the elytra of males (Wittmer, 1963; Brancucci, 1982). Recently, new species were described from southeastern Brazil, and photographs of all known species as well as an identification key for the genus was provided (Biffi, 2015). Additionally, new records for some species considerably extended the distribution range of the genus. It is currently composed of nine species which are widely distributed in South America, from French Guiana to northern Argentina and from Bolivia to the southeastern Brazilian coast (Biffi, 2015; Constantin, 2016). Shortly after the publication of that work, specimens of a new *Paramaronius* species were found among the undetermined specimens from the Naturhistorisches Museum Basel (Switzerland). Here, *Paramaronius unituberculatus* sp. nov., from Argentina, is described and illustrated and the identification key given in Biffi (2015) is updated to include the new species.

MATERIAL AND METHODS

The type specimens of *Paramaronius unituberculatus* sp. nov. are deposited in the Naturhistorisches Museum Basel (NMB) and Museu de Zoologia da Universidade de São Paulo (MZSP). Morphological terminology used in the description follows Biffi (2015) and Brancucci (1982). Photographs were taken with a Canon EOS Rebel T3i camera with Canon MP-E 65mm macro-lens and StackShot macro-

rail. Multi-focus images were combined with Zerene Stacker 1.04. Illustrations and photographs were edited in Adobe Photoshop CS6 and Adobe Illustrator CS6.

TAXONOMY

Paramaronius unituberculatus sp. nov.
Figs 1-12

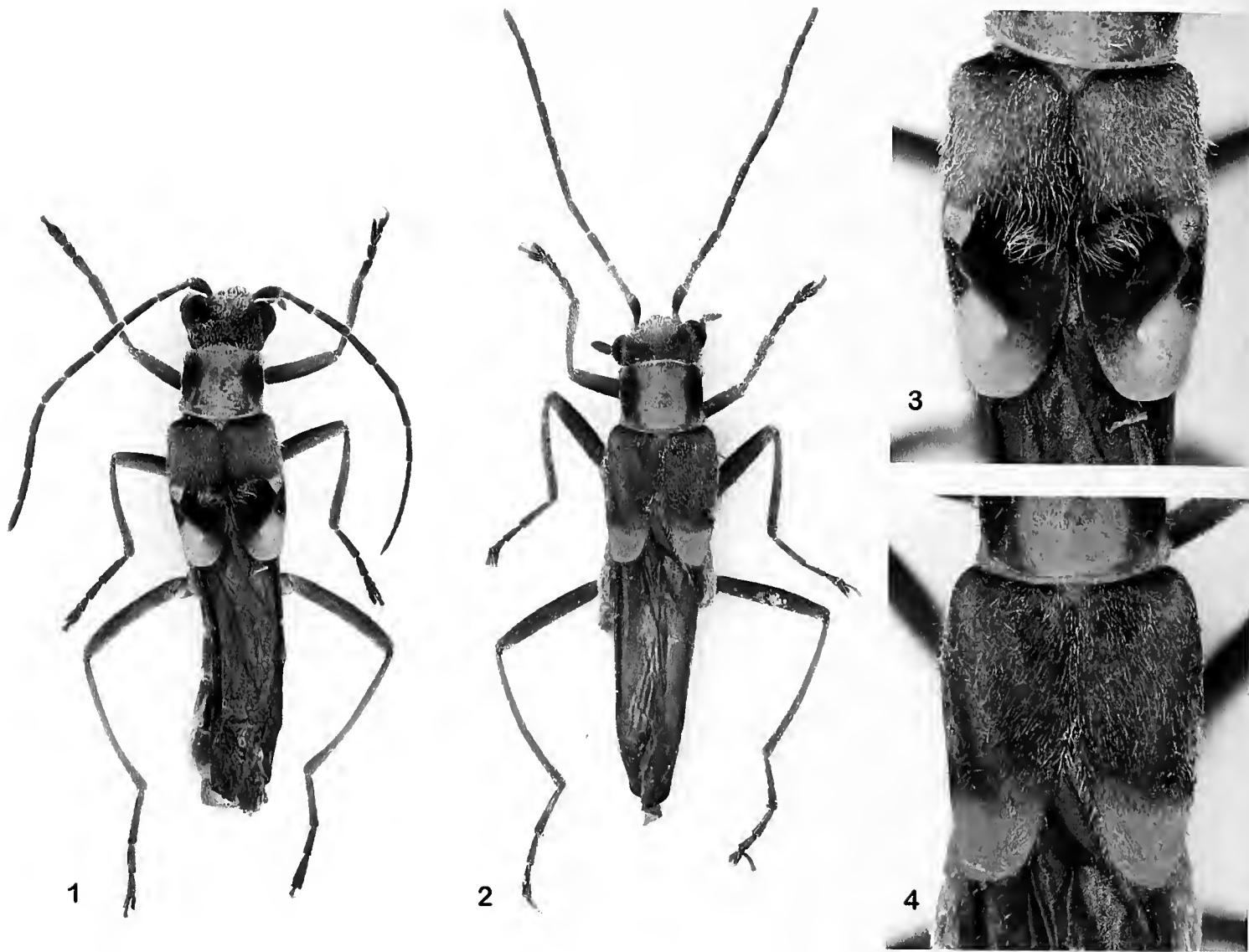
Holotype: NMB, 1♂; ARGENTINA, Salta, Salta (Cerro San Bernardo), 8.ii.1982, 1450 m, H & A Howden.

Paratypes: MZSP 7062; 1♀; ARGENTINA, Salta, i.1949, Wigodzinsky. – NMB; 1♀ Amblayo, ii.1945.

Diagnosis: *Paramaronius unituberculatus* sp. nov. is characterized by the single apical tubercle in the elytra of males and by the shapes of aedeagus and the seventh ventrite of males and females.

Etymology: The specific epithet is a derivative of the Latin words *unus* (one) + *tuberculatum* (tuberculate), referring to the single tubercle on the apex of each elytron.

Description: Head occipital region, center of clypeus and apex of mandibles light to dark brown; vertex, frons, sides of clypeus, genae and base of mandibles pale yellow; antennae light to dark brown, lighter on ventral side of three proximal antennomeres. Labial and maxillary palpi light brown, darker on last palpomeres. Pronotum pale yellow with two large dark brown lateral patches. Scutellum pale yellow. Elytra dark brown with yellow apical patch. Hind wings dark brown. Thorax



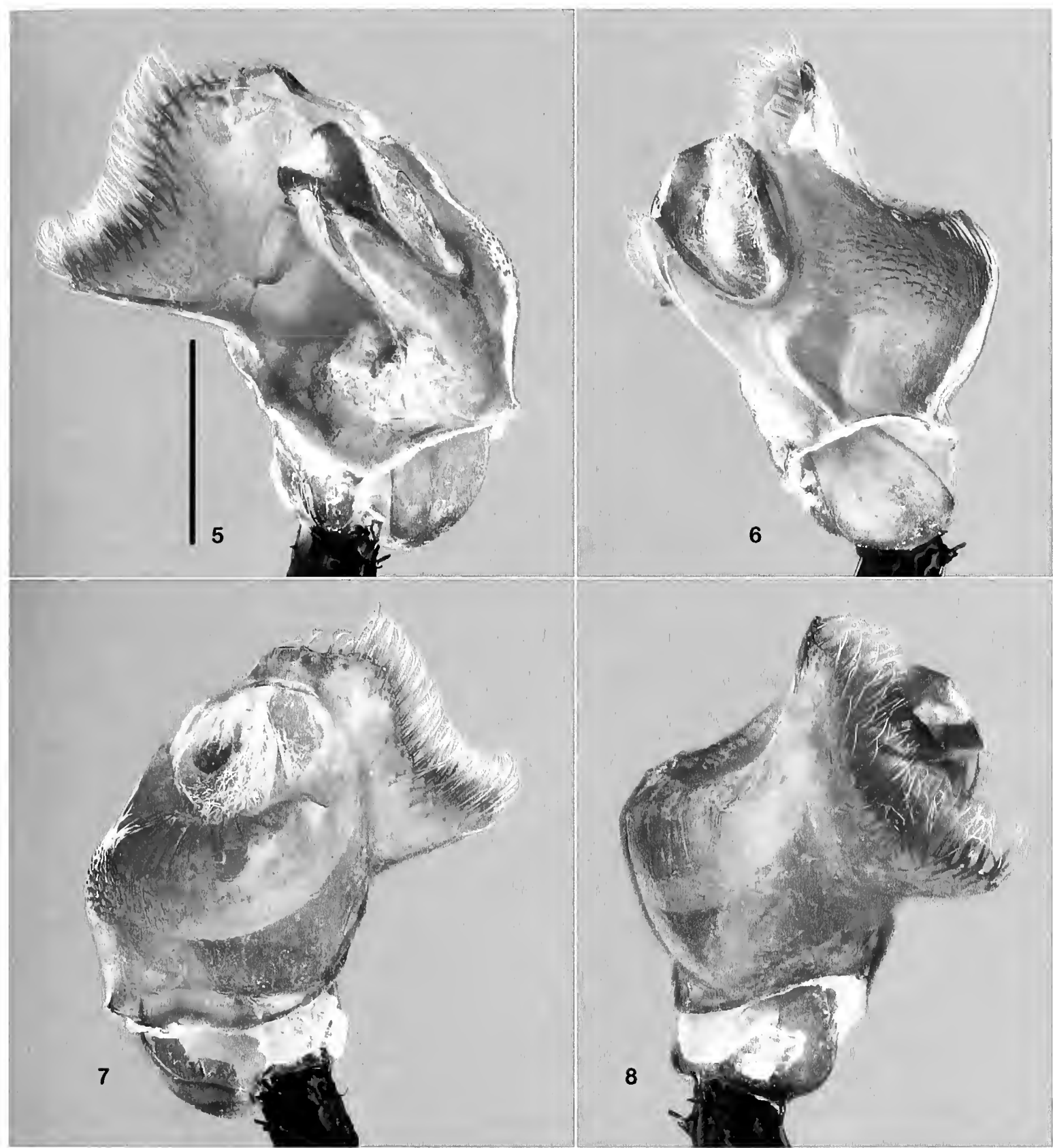
Figs 1-4. *Paramaronius unituberculatus* sp. nov. (1) Dorsal habitus of male (holotype, NMB). (2) Dorsal habitus of female (paratype, MZSP). (3) Detail of the elytra of male. (4) Detail of the elytra of female.

and legs light brown, darker on the dorsal surface of femora and pro- and mesothoracic tarsi. Abdomen dark brown, yellow on the margins of each ventrite and tergite; last ventrite completely brown.

Male (Fig. 1): head densely pubescent; vertex and occipital region flat, lateral margins slightly arcuate behind the eyes. *Antennae* long, with two antennomeres surpassing the apex of elytra; antennomere I slightly swollen apically, antennomere II three times shorter than I, antennomere III twice longer than II, antennomeres IV-VIII subequal in length, slightly longer than I, antennomeres VIII-XI progressively decreasing in length towards the apex. *Pronotum* as long as wide; anterior and posterior margins rounded; lateral margins slightly sinuate; anterior and posterior angles directed upwards. *Scutellum* triangular, apex widely rounded. *Elytra* (Fig. 3) densely pubescent, short, each elytron 2.6 times longer than wide; internal margins dehiscent from apical half, apex rounded; each elytron with a deep and broad hollow meeting medially; a dense fringe of long setae on the anterior wall and margin of hollows; dorsal surface with a large apical tubercle. *Legs* slender; tibiae longer than femora; tarsomeres

gradually increasing in size from pro- to metathoracic leg; first metatarsomere 1.85 times longer than second and 3.65 times longer than third. *Abdomen*: abdominal glandular pores slightly prominent. Seventh abdominal ventrite (Fig. 9) slightly wider than long, pubescent, distal margin slightly emarginated laterally and strongly emarginated and rounded at middle. *Aedeagus* (Fig. 5-8) with a large right prolongation of tegmen, broadly sinuous on posterior margin, covered with long and thick setae; base and dorsal surface with projecting apophysis; left setiferous prolongation long and curved, slightly clubbed, with few setae at apex; right paramere (Fig. 11) long, curved, narrowing upwards and divided in two opposite processes reaching both apophysis of tegmen; left paramere flat, long, divided apically and covering the base of dorsal surface of median lobe; median lobe long and slightly curved to the right; left surface of tegmen rough.

Female (Fig. 2): slightly smaller than the male; eyes smaller and more rounded; dorsal surface of elytra (Fig. 4) without sculptural modifications; seventh abdominal ventrite (Fig. 10) narrowed apicad, distal



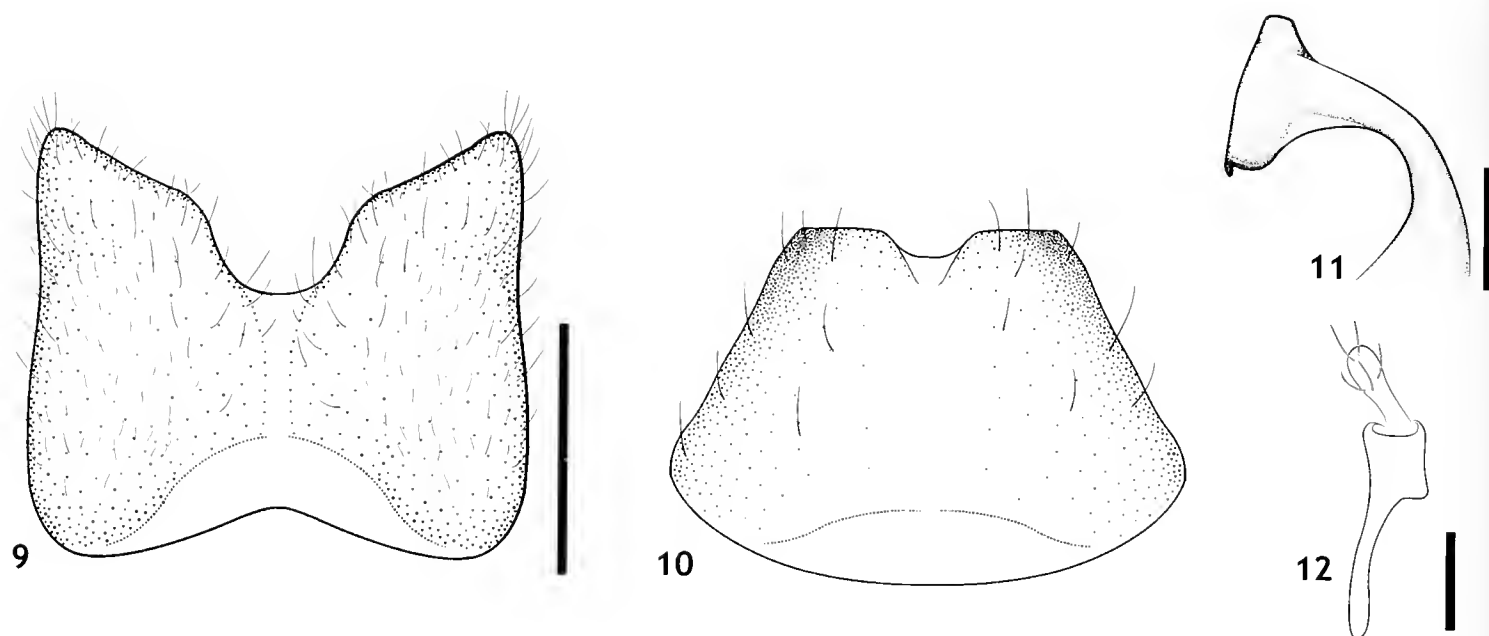
Figs 5-8. Aedeagus of *Paramaronius unituberculatus* sp. nov. (holotype, NMB). (5) Dorsal view. (6) Left view. (7) Ventral view. (8) Right view. Scale = 0.5 mm.

margin almost straight and with a small notch at middle; coxites (Fig. 12) small and membranous, base long and slender; styles short, wider apically.

Dimensions: Total length 7.5-9.0 mm.

Remarks: *Paramaronius unituberculatus* sp. nov. is similar to *P. kraatzi* (Pic, 1938) and *P. freyi* Wittmer, 1963 in the typical elytral sculpture and in the rugosity

on the left surface of the tegmen. It differs from these species by the colouration of head, antennae, pronotum and legs, apex of elytra with just one tubercle (two tubercles in *P. kraatzi* and three in *P. freyi*), shape of seventh abdominal ventrite of males and females, shape of aedeagus and parameres, and less roughness of tegmen. Males of *P. impressipennis* (Pic, 1906), from Argentina and Brazil, differ from *P. unituberculatus*



Figs 9-12. *Paramaronius unituberculatus* sp. nov. (9) Seventh ventrite of the male (holotype, NMB). (10) Seventh ventrite of the female (paratype, MZSP). (11) Right paramere of aedeagus (holotype, NMB). (12) Right coxite of female (paratype, MZSP). Scales: 9-10 = 0.5 mm, 11-12 = 0.2 mm.

sp. nov. by the presence of elytra with one longitudinal ridge on posterior half, without deep grooves and tubercles. Females differ especially by the shape of distal margin of the last abdominal ventrites.

The most recent identification key (Biffi, 2015) has to be modified to include the new species as follows:

- 4 Head, pronotum and legs completely testaceous; antennae testaceous, darker from antennomere 7 to apex; males: each elytron with one median and two apical tubercles *P. kraatzii* (Pic)
- Head dark brown to black; pronotum completely yellow or with two brown patches on lateral margin; males: each elytron with one or three apical tubercles **4a**
- 4a** Head black; pronotum completely yellow or with two brown spots on lateral margins; legs yellow with brown spots on apex of femora and tibiae, tarsi brown; antennae brown, slightly lighter on two first and three last antennomeres; males: each elytron with one median and three apical tubercles *P. freyi* Wittmer
- Head dark brown; pronotum with two brown spots on lateral margins; legs light brown, darker on dorsal surface of femora, tarsi brown; antenna completely dark brown; males: each elytron with low median and apical tubercle (Fig. 3) *P. unituberculatus* sp. nov.

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**A revision of the Chilean Brachyglutini – Part 2. Revision of *Achilia* Reitter, 1890:
A. crassicornis, *A. tumidifrons*, *A. bifossifrons*, and *A. lobifera* species groups
(Coleoptera: Staphylinidae: Pselaphinae)**

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Abstract

The *Achilia crassicornis*, *A. tumidifrons*, *A. bifossifrons*, and *A. lobifera* species groups (*sensu* Jeannel, 1962) of the species-rich genus *Achilia* Reitter, 1890 are revised. Of the twelve taxa previously placed in these four groups of species, two belong to different groups and will be treated in later papers (i.e. *A. parvula* Jeannel, 1962 and *A. nahuelbutae* Franz, 1996 with the *A. humidula* and the *A. cosmoptera* groups, respectively), and five names are placed as junior synonyms: *Achilia crassicornis antarctica* Jeannel, 1962 and *A. obscura* Jeannel, 1962 = *A. crassicornis* Jeannel, 1962 (**syn. nov.**); *Achilia tumidifrons* Jeannel, 1962, *A. globiceps* Jeannel, 1962 and *A. paraglobiceps* Franz, 1996 = *A. larvata* (Reitter, 1885) (**syn. nov.**). The lectotype and paralectotypes of *A. larvata* are designated. The five species left in these groups are redescribed, their distributions are detailed, and habitats/collecting data are summarized.

Keywords: *Achilia* - Chile - species group - taxonomy - distribution.

INTRODUCTION

This article is the second contribution in a series dedicated to a taxonomic revision of the Brachyglutini of the temperate region of southern South America. After an overview of the taxonomic situation within the tribe, and a preliminary diagnosis of the species-rich genus *Achilia* Reitter (Kurbatov & Sabella, 2015), we here focus on the *Achilia crassicornis*, *A. tumidifrons*, *A. bifossifrons*, and *A. lobifera* species groups (*sensu* Jeannel, 1962). Their constitutive members are critically reexamined, and each species left in them is redescribed, its synonymic framework and distribution is detailed, and collecting data are summarized. The maintainence of these species groups of *Achilia*, which are mainly based on male sexual dimorphisms, as well as their possible phylogenetic relationships will be reassessed later.

MATERIAL AND METHODS

This study is based on the examination of 6008 specimens.

The acronyms used in the present study refer to the following collections (relevant curator/collection manager acknowledged in parenthesis):

- DBUC Department of Biological, Geological and Environmental Sciences, University of Catania, Italy
- FMNH Field Museum of Natural History, Chicago, U.S.A. (J. H. Boone)
- HNMB Hungarian National Museum, Budapest, Hungary (Gy. Makranczy)
- MHNG Muséum d'Histoire Naturelle, Genève, Switzerland
- MNHN Muséum National d'Histoire Naturelle, Paris, France (T. Deuve and A. Taghavian)
- MNHS Museo Nacional de Historia Natural, Santiago, Chile (M. Elgueta Donoso and Y. J. Sepulveda Guaico)
- MSNG Museo Civico di Storia Naturale "G. Doria", Genova, Italy (R. Poggi)
- NHMW Naturhistorische Museum, Wien, Austria (H. Schillhammer)
- PHPC Private collection of Peter Hlavác, Prague, Czech Republic (P. Hlavác)

UNHC University of New Hampshire Arthropod Collection, Durham, NH, U.S.A. (D.S. Chandler)

Under the sections “type material” or “additional material” the locality data are standardized, with indications of major administrative units (regions and provinces) and names of collectors in parentheses. When species were described from more than one specimen, Jeannel (1962) used to mention the locality of the “type” (i.e. holotype) with its depository, followed by the depository(s) of the paratypes. For example at page 399 for *Achilia crassicornis* he states “type: Puerto Eden (Musée de Santiago) (paratypes au Muséum de Paris)”; however in the loaned material we received, topotypic specimens labelled as paratypes were present at both institutions, as well as from other localities listed by Jeannel in the distribution of the taxon. We decided to apply a restrictive interpretation of Jeannel’s statements, and list all the specimens mislabelled as paratype under “additional material” according to our interpretation.

The body length is measured from the anterior clypeal margin to the posterior margin of the last visible abdominal tergite. The length and width of the body parts were measured between points of maximum extension, e.g. the head length is measured between the anterior clypeal margin and the posterior margin of the neck; the head width includes the eyes, the elytral length along the suture line, and the elytral width is the total width of the two elytra taken together. The abdominal tergites are numbered based on order of visibility. Morphological terminology follows that of Chandler (2001), except that the abdominal sternites are termed ventrites here.

TAXONOMY

Genus *Achilia* Reitter, 1890

Achilia Reitter, 1890: 212 (new name for *Bryaxis* Raffray, 1890)

Bryaxis Raffray, 1890: 123 (preoccupied, not Reitter, 1880).

Achillia Raffray, 1904: 113 (misspelling).

Clermontodes Jeannel 1950: 317.

Reitter (1890) introduced the generic name *Achilia* in replacement of *Bryaxis* Raffray, 1890, which was preoccupied by *Bryaxis* Reitter, 1880. *Achilia* was however consistently misspelled as *Achillia* since Raffray (1904) and subsequent authors until Newton & Chandler (1989), pointed out the correct original spelling.

Achilia crassicornis species group

Jeannel (1962: 397, 400) characterized this group as follows: elytra with 3 basal foveae; basal striae of abdominal tergite I separated at most by 1/3 of tergal

width; head with broad transverse occipital hump in male; frons not narrowed anteriorly in female; male antennomere X very big and asymmetrical; copulatory pieces of aedeagus thin.

This group currently includes *A. crassicornis antarctica* Jeannel, 1962; *A. crassicornis crassicornis* Jeannel, 1962; *A. obscura* Jeannel, 1962; *A. parvula* Jeannel, 1962, and *A. nahuelbutae* Franz, 1996. However, as *A. parvula* and *A. nahuelbutae* appeared to belong to the *humidula* and the *cosmoptera* groups respectively, and *A. crassicornis antarctica* and *A. obscura* are here placed as junior synonyms of *A. crassicornis*, the only taxon left in the *crassicornis* species group is *A. crassicornis* itself.

Achilia crassicornis Jeannel, 1962

Figs 1-11, 21, 24, 31

Achilia crassicornis crassicornis Jeannel, 1962: 399, figs 144 (habitus) and 146 (aedeagus). – Franz, 1996: 114, fig. 61 (aedeagus).

Achilia crassicornis antarctica Jeannel, 1962: 399, fig. 145 (aedeagus). – Franz, 1996: 114 **syn. nov.**

Achilia obscura Jeannel, 1962: 401 **syn. nov.**

Type material (41 ex.): SOUTHERN CHILI: Región Magallanes y de la Antártica Chilena: Antártica Chilena prov.: MHNS; 1 ♂ (holotype of *Achilia crassicornis antarctica* n° 1623); Navarino Island, Puerto Williams; 31.I.1957; G. Kuschel. – MNHN; 12 ♂ and 18 ♀ (paratypes of *Achilia crassicornis antarctica*); Navarino Island, Puerto Williams; 54° 56’S; 31.I.1957; G. Kuschel; *Nothofagus betuloides* and *Nothofagus pumilio* forest. – Última Esperanza prov.: MHNS; 1 ♂ (holotype of *Achilia crassicornis crassicornis* n° 1575); Puerto Eden; 06.XII.1958; G. Kuschel. – MNHN; 6 ♂ and 2 ♀ (paratypes of *Achilia crassicornis crassicornis*); Wellington Island, Puerto Eden, Carlos Islet; 49° 09’S; 06.XII.1958; G. Kuschel; *Nothofagus betuloides* dense forest. – MNHN; 1 ♀ (holotype of *Achilia obscura*; according to the original description the holotype of *A. obscura* should have been deposited in MHNS, however we found it in MNHN); Wellington Island, Puerto Eden, Carlos Islet; 49° 09’S; 600 m; 6.XII.1958; *Nothofagus betuloides* forest.

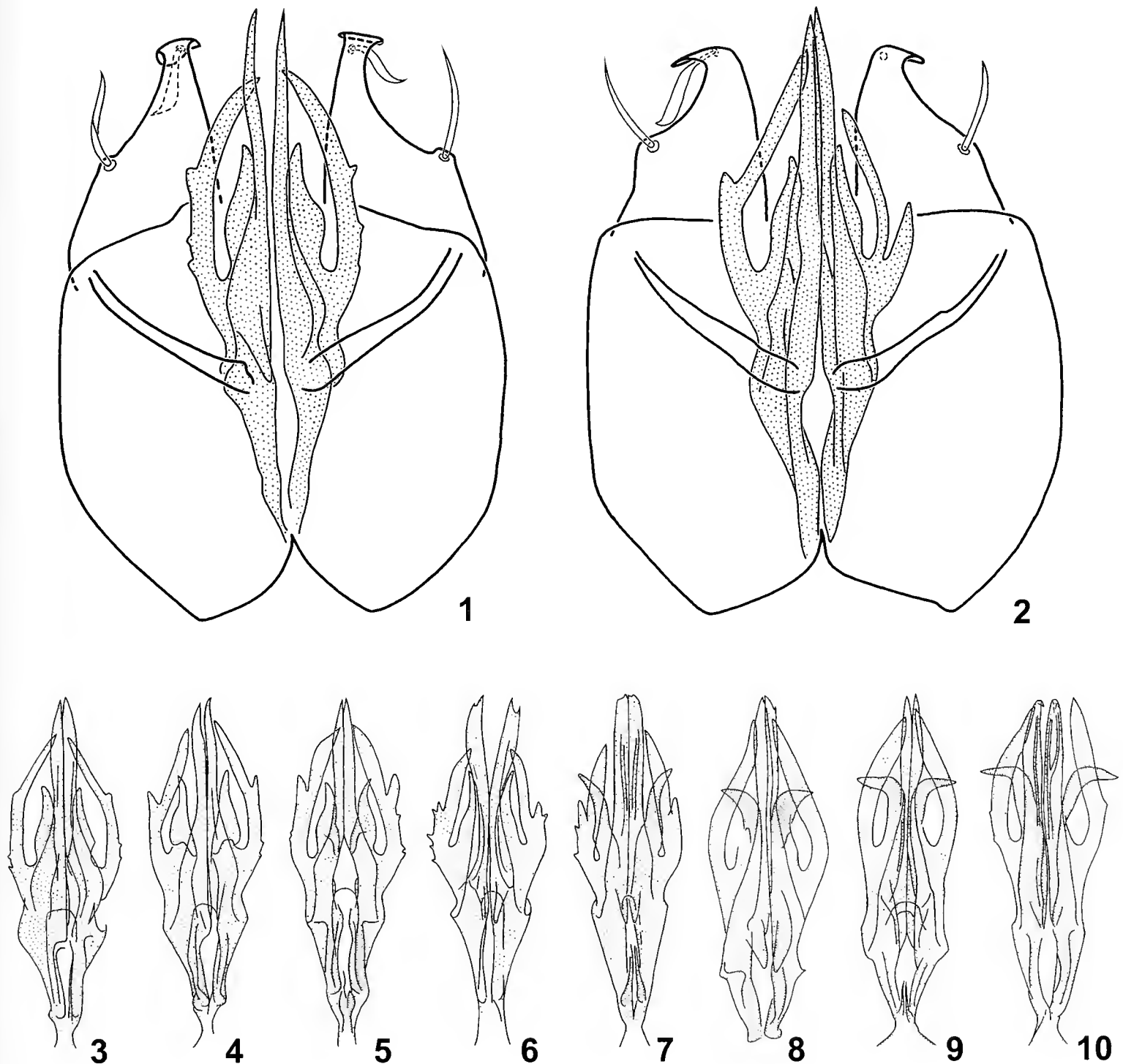
Additional material (2166 ex.): See Appendix 1.

Description: Body 1.50-1.75 mm long, reddish brown with head and abdomen sometimes slightly darker and palpi yellowish. Pubescence decumbent with dense and long setae, uniform on entire body. Head wider than long; frontal lobe short with rounded sides; surface smooth, shiny, with some minute punctures; vertexal sulcus deeply impressed and narrowed in middle; vertexal foveae shallow and large; eyes protruding, longer than convex temples. Pronotum wider than long and wider than head; posterior portion of lateral outlines sinuate; disc smoothly convex, shiny, with

some small punctures; basal margin bordered with row of contiguous shallow impressions; median antebasal fovea smaller than lateral foveae. Elytra together wider than long with protruding humeri; disc smooth, shiny, with some small punctures; generally four basal foveae (two lateral foveae very close) or occasionally three (lateral foveae consisting of two combined foveae); sutural stria entire; discal stria extending to about elytral midlength. Legs slender. Abdomen smooth,

shiny, with some minute punctures; tergite I with basal striae slightly diverging, extending to about one-third of paratergal length, separated at base by about one-third of tergal width, with short and sparse setal brush between striae.

Male: Head as in Figs 21 & 24, with occiput strongly convex. Antennae (Fig. 11) with scape distinctly longer than wide; pedicel slightly longer than wide; antennomeres III-VIII small and slightly transverse;



Figs 1-10. Aedeagi (1-2) and variability of the internal sac (3-10) of *Achilia crassicornis*. (1) *A. crassicornis crassicornis*, paratype from Puerto Eden, Última Esperanza province. (2) *A. crassicornis antarctica*, paratype from Puerto Williams, Antártica Chilena province. (3) specimen from Cerro Castillo Natural Reserve, Coihaique province. (4) specimen from Ushuaia Mount San Martial, Tierra del Fuego province. (5) specimen from Aguas Calientes to Antillanca, Osorno province. (6) specimen from Playa Linda, Cautín province. (7) specimen from Conquillo National Park, Cautín province. (8) specimen from San Pedro, Chiloé province. (9) specimen from Cucao, Chiloé province. (10) specimen from Chiloé National Park, Chiloé province.

antennomere IX strongly transverse with protruding mesal margin; antennomere X strongly thickened, wider and longer than XI, medial side truncate with broad subtriangular fairly flat area entirely delimited by sharp low ridge and covered with short dense pubescence. Metasternum convex; ventral margin of mesotrochanters with small acute lateral spine; all tibiae unarmed. Abdominal tergites unmodified; ventrites IV-V slightly flattened at middle. Aedeagus (Figs 1-2) 0.39-0.41 mm long; dorsal plate ovoid with rounded sides and diverging dorsal strips starting from middle of dorsal plate; copulatory pieces each divided into two simple or bifurcated spreading branches slightly variable in shape (Figs 1-10). Parameres with outer outline only slightly convex or fairly straight at level of middle seta; tips narrow recurved internally.

Female: Similar to male except: head with occiput broadly convex, not swollen; antennomeres X and XI less wide than in male, X with medial side not truncate and shorter than XI; mesotrochanters and abdominal ventrites unmodified.

Collecting data: Collected from September to March, mainly in *Nothofagus* forests, but also in *Araucaria*, *Saxegothaea conspicua* and *Fitzroya cupressoides* forests, where it was found in remnants of forests or at their edges at elevations ranging from sea level up to 1500 m and the treeline. Most specimens came from sifted samples of leaf and log litter, moss, dead trunks,

vegetable debris, and sometimes mushrooms, but other collecting techniques include car netting, flight intercept (window) traps, malaise traps, carrion traps, pan traps, and screen sweeping. Jeannel (1962) mentions specimens collected wandering on the sandy shores of Lacar Lake (Argentina, Neuquén province).

Distribution: *Achilia crassicornis* is distributed (Fig. 31) from the southernmost regions of Chile and Argentina to Central Chile (northernmost province: Ñuble) and Central Western Argentina (northernmost province: Neuquén). Records from Chepu (Chiloé prov.) come from Jeannel (1962). According to Jeannel (1962) it is the only species of *Achilia* to be so widespread in the Valdivian and Magellanes forests.

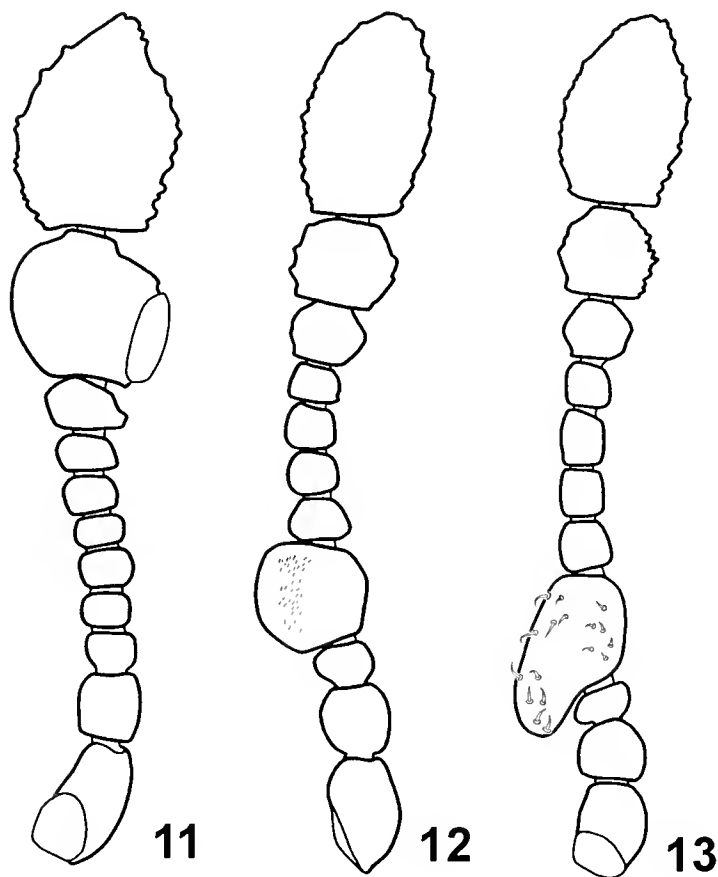
Comments: The holotype and only known specimen of *A. obscura* should be in the MHNS collection according to Jeannel (1962: 401, but it is in the MNHN collection. Moreover, in the catalog of the MHNS holotypes of insects (Camousseight, 1980) this taxon is not mentioned. Jeannel (1962) described *A. antarctica* as a subspecies of *A. crassicornis* that was characterized by having the pronotum barely transverse, the aedeagus larger with shorter paramere apices, and the internal sac with stouter copulatory pieces. He also described the new species *A. obscura* to accomodate specimens differing from *A. crassicornis* by having the body darker and slightly longer, as well as the basal striae of abdominal tergite I more narrowed. However, after examining abundant materials we concluded that these differences were overestimated and pertain to intraspecific variation, and consequently place here both *A. crassicornis antarctica* Jeannel, 1962 and *A. obscura* Jeannel, 1962 as junior synonyms of *A. crassicornis* Jeannel, 1962 (**syn. nov.**).

Two males from Chiloé Island (San Pedro and Cucao) have the antennomeres X narrower with their medial side not truncate, but their aedeagi are similar to that of the other males of *A. crassicornis* that we examined, and the shape of their copulatory pieces (Figs 8-9) fall within the range of intraspecific variation that we observed for this structure.

Achilia parvula Jeannel, 1962

Achilia parvula Jeannel, 1962: 401.

Comments: According to the original description the holotype and only known specimen of *A. parvula* should have been deposited in the MHNS, however we found it in the MNHN. In the catalog of the MHNS holotypes of insects (Camousseight, 1980) this taxon is not mentioned. It appears to be a female of the *humidula* group, which will be dealt with in a later paper.



Figs 11-13. Male antennae of *Achilia*. (11) *A. crassicornis*. (12) *A. antennalis*. (13) *A. lobifera*.

***Achilia nahuelbutae* Franz, 1996**

Achilia nahuelbutae Franz, 1996: 115, fig. 62 (aedeagus).

Comments: We have examined the type series of this species, which is housed in NHMW. The holotype appears to be a male of the *cosmoptera* group, while paratypes belong to at least two other *Achilia* species of the *kindermanni* and the *grandiceps* groups, and includes a specimen of the tribe Euplectini. All of these taxa except the member of the Euplectini will be dealt with in a later paper.

***Achilia tumidifrons* group**

Jeannel (1962: 398, 402) characterized this group as follows: elytra with 2 basal foveae; basal striae of abdominal tergite I separated by $1/3$ of tergal

width; head with broad transverse occipital hump in male; frons not narrowed anteriorly in female; male antennomere X not enlarged; copulatory pieces of aedeagus thin.

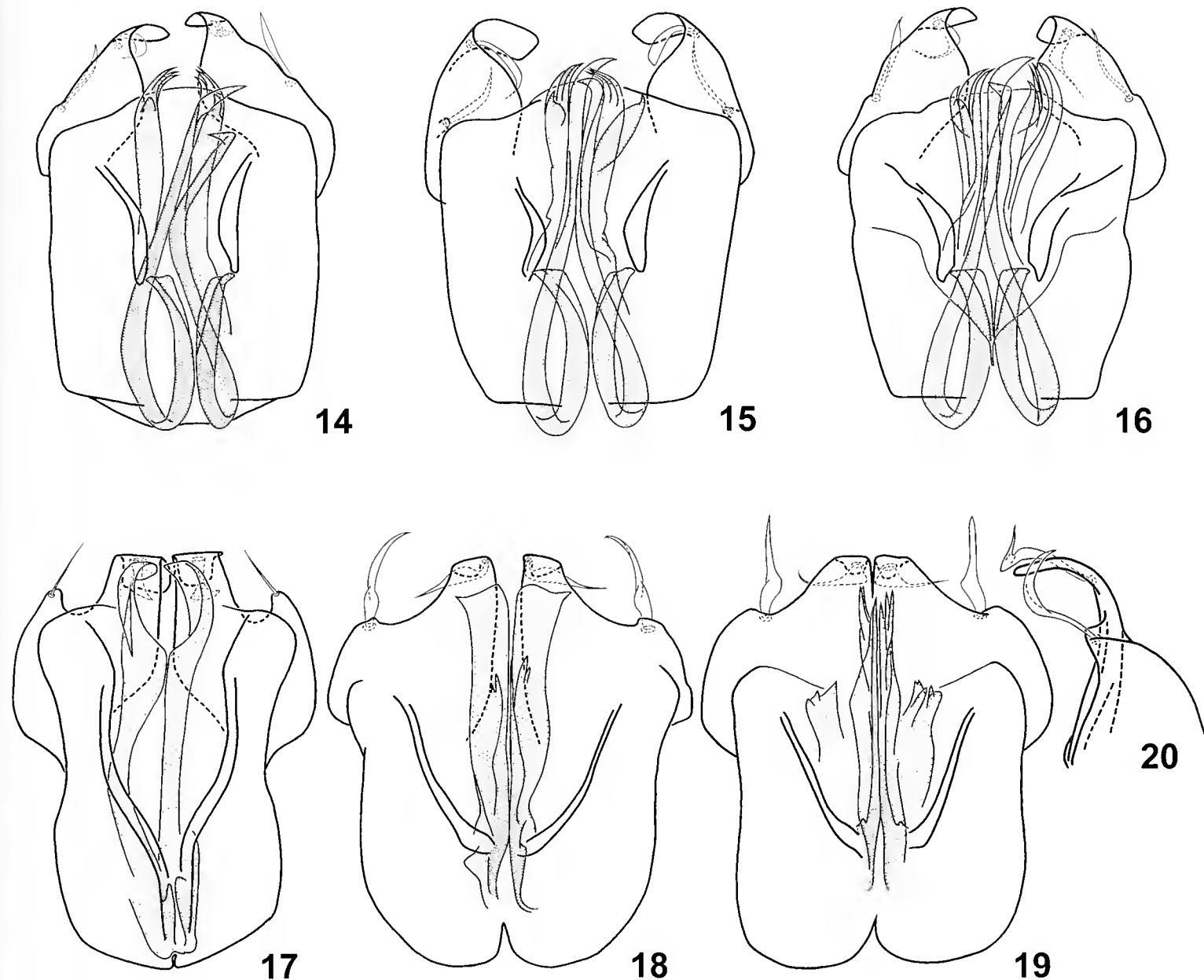
The group currently includes *A. larvata* (Reitter, 1885), *A. tumidifrons* Jeannel, 1962, *A. globiceps* Jeannel, 1962, and *A. paraglobiceps* Franz, 1996. However, we place all of these names as *A. larvata*, becoming the only constitutive member in the unfortunately named *tumidifrons* group.

***Achilia larvata* (Reitter, 1885)**

Figs 14-16, 22, 25, 32

Bryaxis larvata Reitter, 1885: 330, pl. 2, fig. 15 (head and antenna).

Achilia larvata, Jeannel, 1962: 402, 403 fig. 149 (aedeagus).



Figs 14-20. Aedeagi (14-19) and the left paramere in lateral view (20) of *Achilia*. (14) *A. tumidifrons*, paratype from Chepu, Chiloé province. (15) *A. larvata*, lectotype from environs of Valdivia, Valdivia province. (16) *A. globiceps*, paratype from Frutillar, Llanquihue province. (17) *A. bifossifrons*, specimen from Salto Petrohué, Llanquihue province. (18) *A. lobifera*, specimen from Aguas Calientes, Osorno province. (19-20) *A. antennalis*, specimen from Princesa, Osorno province.

Achilia tumidifrons Jeannel, 1962: 402 figs 147 (habitus), 148 (aedeagus). – Franz, 1996: 115 **syn. nov.**

Achilia globiceps Jeannel, 1962: 402, 403 fig. 50 (aedeagus). – Franz, 1996: 115 **syn. nov.**

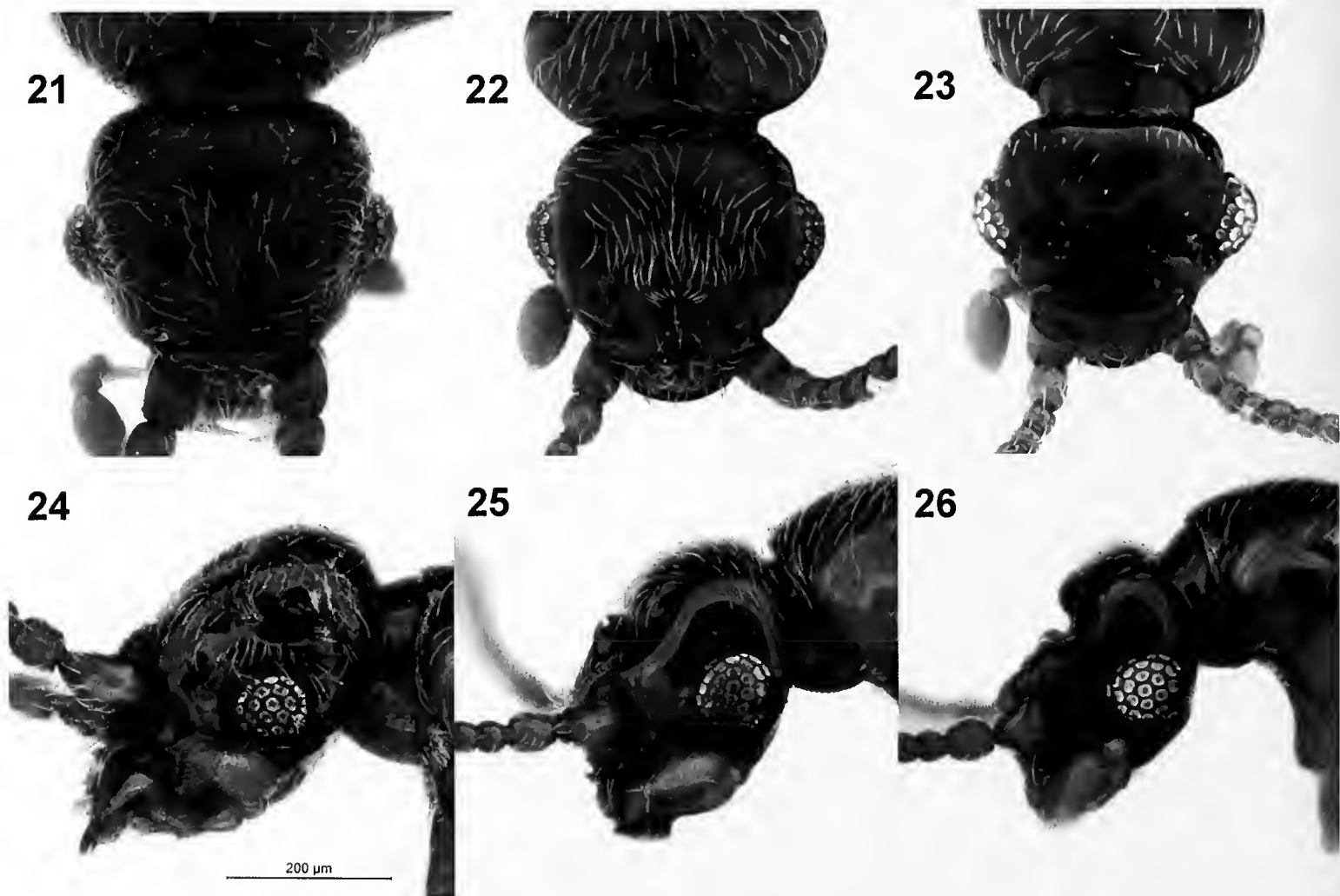
Achilia paraglobiceps Franz, 1996: 115 fig. 63 (aedeagus) **syn. nov.**

Type material (75 ex.): CENTRAL CHILI: Región Los Lagos: Chiloé prov.: MHNS; 1 ♂ (holotype of *Achilia tumidifrons* n° 1626); Chepu; 03.X.1958; G. Kuschel. – MNHN; 3 ♂ and 1 ♀ (paratypes of *A. tumidifrons*); Chepu; 42° 03'S; 02.X.1958; G. Kuschel; forest. – MNHN; 1 ♀ (paratype of *A. tumidifrons*); Chepu; 42° 03'S; 03.X.1958; G. Kuschel; forest. – MNHN; 1 ♀ (paratype of *A. tumidifrons*); Chepu; 42° 03'S; 04.X.1958; G. Kuschel; forest. – MNHN; 1 ♂ (paratype of *A. tumidifrons*); Chepu; 42° 03'S; 07.X.1958; G. Kuschel; forest. – MNHN; 2 ♀ (paratypes of *A. tumidifrons*); Chepu; 42° 03'S; 09.X.1958; G. Kuschel; forest. – MNHN; 2 ♂ and 11 ♀ (paratypes of *A. tumidifrons*); Chepu; 42° 03'S; 15.X.1958; G. Kuschel; forest. – MNHN; 5 ♂ and 3 ♀ (paratypes of *A. tumidifrons*); Chepu; 42° 03'S; 16.X.1958; G. Kuschel; Llanquihue prov.: MHNS; 1 ♂ (holotype of *Achilia globiceps* n° 1646); Frutillar; 20.IX.1954; G. Kuschel. – MNHN; 9 ♂ and 23 ♀ (paratypes of *A.*

globiceps); Frutillar; 41° 08'S; 20.IX.1954; G. Kuschel. – Osorno prov.: NHMW; 1 ♂ (holotype of *Achilia paraglobiceps*); Puyehue National Park, Osorno, 1 km above the forestal house; 23.IX.1965; H. Franz; litter sifting in laurel forest. – Región Los Ríos: Valdivia prov.: MNHN (coll. Raffray); 9 ♂ (lectotype and paralectotypes of *Achilia larvata* here designated); Chili – HNMB; 1 ♀ (paralectotype of *Achilia larvata* here designated); Valdivia.

Additional material (1284 ex.): See Appendix 1.

Description: Body 1.25–1.40 mm long, reddish with darker head and abdomen, antennae, palpi and legs yellow-reddish. Pubescence decumbent with dense and long setae, uniform on entire body. Head wider than long; frontal lobe flattened with rounded sides; surface smooth, shiny, with some minute punctures; vertexal sulcus impressed; vertexal foveae shallow and large; eyes protruding, longer than convex temples. Pronotum wider than long and as wide as head, with maximal width on anterior half; posterior portion of lateral outlines sinuate; disc strongly convex, smooth and shiny; median antebasal fovea smaller than lateral foveae; basal margin bordered with row of contiguous shallow impressions. Elytra together wider than long



Figs 21–26. Head in dorsal (21–23) and lateral (24–26) views. (21, 24) *A. crassicornis*. (22, 25) *A. larvata*. (23, 26) *A. bifossifrons*. (24).

with protruding humeri; disc smooth, shiny, with some minute punctures; three basal foveae (lateral fovea consisting of two combined foveae); sutural stria entire; discal stria extending to about elytral midlength. Legs slender. Abdomen smooth, with some minute punctures; tergite I with basal striae slightly diverging, extending to about one-third of paratergal length, separated at base by about one-third of tergal width, with short and sparse setal brush between striae.

Male: Head as in Figs 22 & 25; width and convexity of occipital area variable, from conformation very similar to that in female to conspicuously swollen. Antennae with scape slightly longer than wide; pedicel distinctly longer than wide; antennomeres III-VIII small and slightly transverse; antennomere IX strongly transverse; antennomere X strongly transverse, wider than IX, bearing conspicuous subapical tooth; antennomere XI elongate and as long as VII-X combined. Metasternum with narrow medial sulcus; ventral margin of mesotrochanters with small acute lateral spine; mesotibiae slightly enlarged on distal third and distinctly indented subapically. Abdominal tergites and ventrites unmodified. Aedeagus (Figs 14-16) 0.28-0.30 mm long; dorsal plate subrectangular with dorsal strips reduced in comparison with those in the other species treated here; copulatory

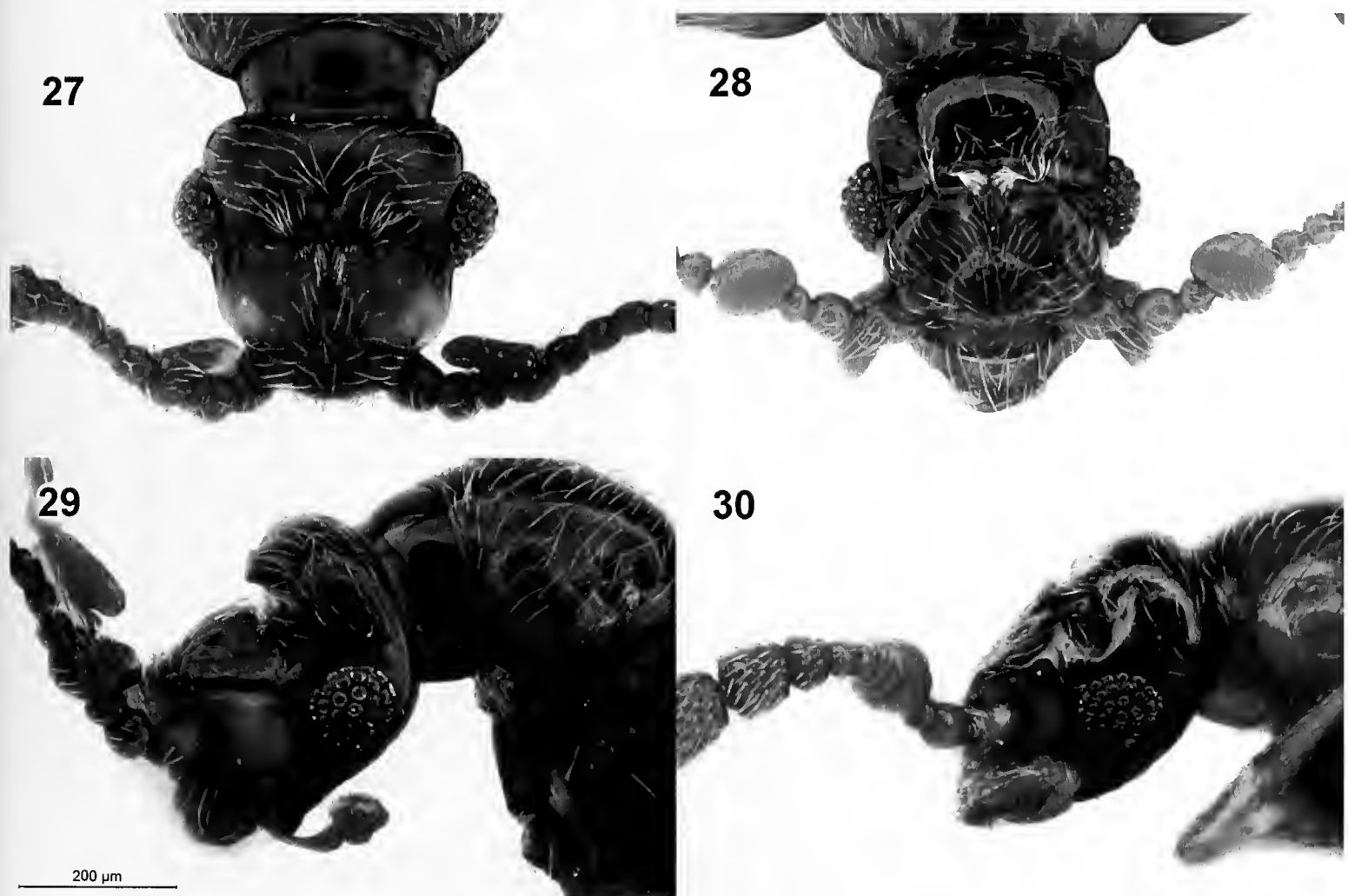
pieces consisting of pair of long medial sclerites curved at base and apically pointed, with pair of short lateral sclerites apically trifurcated. Parameres not expanded in with outer outline only slightly convex or fairly straight at level of middle seta; tips broadly recurved internally.

Female: Similar to male except: head narrower with occiput broadly convex; antennomere XI shorter, not longer than VIII-X combined; mesotrochanters and mesotibiae unmodified.

Collecting data: Collected from September to March, mainly in *Nothofagus* / *Podocarpus* mixed forests at elevations ranging from sea level up to 700 m. Most specimens came from sifted samples of leaf and log litter, moss, branches, dead trunks, mushrooms, and other vegetable debris, but also were taken by flight intercept (window) and carrion traps.

Distribution: *Achilia larvata* is distributed in Central Chile from Chiloé northward to Ñuble provinces (Fig. 32).

Comments: According to Jeannel (1962) *A. tumidifrons* differs from *A. larvata* by a larger antennal club with antennomere XI two times as wide and four times as long as X (instead of just a little wider and three times longer than X in *A. larvata*), eyes shorter than temples



Figs 27-30. Head in dorsal (27-28) and lateral (29-30) views. (27, 29) *A. lobifera*. (28, 30) *A. antennalis*.

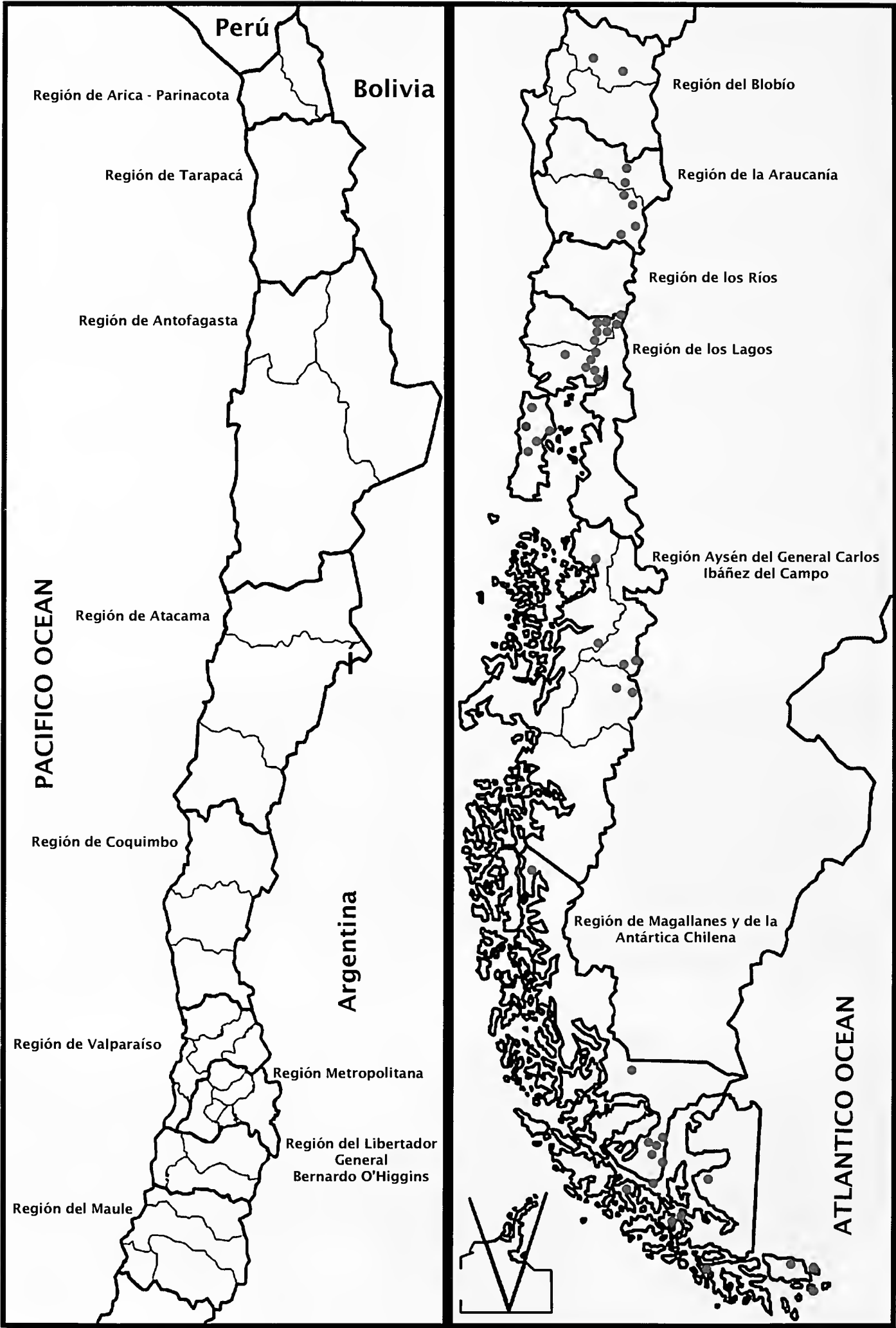


Fig. 31. Distribution map of *Achilia crassicornis* (excluding Argentina) based on examined material.

(instead of longer than temples in *A. larvata*), the frontal tuberosity of male punctate (while smooth in *A. larvata*), the aedeagus with dorsal strips sinuate (while “not sinuate” in *A. larvata*), and parameres with apical part narrow, sides parallel to truncate apex (instead of apical part broad, with outer outlines slightly convergent and apically recurved in *A. larvata*). However, the aedeagal conformation of their types is very similar (Figs 14-15), and after examination of extensive materials it turned out that all these differences (when really present) have been strongly exaggerated by Jeannel and fall according to us within the intraspecific variation of this taxon. Therefore we conclude that *A. tumidifrons* Jeannel, 1962 must be considered as a junior synonym of *A. larvata* (Reitter, 1885) (**syn. nov.**).

Jeannel (1962) distinguished *A. globiceps* from *A. larvata* by its very small antennomeres X and very large antennomeres XI, and above all by a different aedeagal morphology (notably copulatory pieces far less developed, slender and bifurcated, and parameres tapering to apex recurved internally). However, we failed to observe such differences between the aedeagus of the paratype of *A. globiceps* and that of the lectotype of *A. larvata* (Figs 14 & 16), and here consider *A. globiceps* Jeannel, 1962 to be the junior synonym of *A. larvata* (Reitter, 1885) (**syn. nov.**).

We have also examined all the specimens of *Achilia* from the Franz collection. Only three are labelled “Puyehue National Park, Osorno”, which is the locus typicus of *Achilia paraglobiceps*. Only one was already dissected and, although it doesn’t bear a holotype label, it is certainly the holotype of *A. paraglobiceps*, which is now labeled accordingly. This specimen is identical for external morphology and for the aedeagal characters to *A. larvata*, and we here consider *A. paraglobiceps* Franz, 1996 to be the junior synonym of *A. larvata* (Reitter, 1885) (**syn. nov.**).

Reitter (1885) described *Bryaxis larvata* from the locality of Valdivia but did not indicate the number of specimens he had at hand. According to Jeannel (1962: 403) in MNHN there are 10 specimens of *A. larvata*, however in Raffray’s collection we found only 9 males with the simple locality label “Chili”, and those are treated as syntypes. In the HMNB there is a female of *A. larvata* with the locality label “Valdivia” (handwritten by Reitter) and this female is also treated as a syntype. The male lectotype is designated here from the series in MNHN and bears the labels: //Chili// [red label] Type//*A. larvata* det. Raffray//[red label] LECTOTYPE *Achilia larvata* des. G. Sabella//. The other syntypes mentioned above are designated as paralectotypes.

Achilia bifossifrons group

Jeannel (1962: 397, 404) characterized this group as follows: elytra with 3 basal foveae; basal striae of

abdominal tergite I separated at most by 1/4 of tergal width; head with broad transverse occipital hump in male; frons not narrowed anteriorly in female; male antennomere X not enlarged; copulatory pieces of aedeagus thin. The only member of this group has always been *Achilia bifossifrons*.

Achilia bifossifrons (Reitter, 1883)

Figs 17, 23, 26, 33

Bryaxis bifossifrons Reitter, 1883: 50, pl. 1 fig. 9; Reitter 1885: 325, 329.

Achilia bifossifrons, Jeannel, 1962: 404, figs 151 (head and antenna), 152 (aedeagus).

Type material (1 ex.): CENTRAL CHILI: Región Los Ríos: Valdivia prov.: MNHN (coll. Raffray); 1 ♂ (holotype of *Achilia bifossifrons* here fixed); Chili.

Additional material (1907 ex.): See Appendix 1.

Description: Body 1.25-1.40 mm long, reddish with dark head, pronotum and abdomen, palpi yellowish. Pubescence on head short and suberect, long and decumbent over rest of body. Head wider than long; frontal lobe flattened with rounded sides; surface smooth, shiny, with some minute punctures; vertexal foveae small; eyes protruding, longer than convex temples. Pronotum wider than long and as wide as head, width maximal at middle; posterior portion of lateral outlines sinuate; disc strongly convex, smooth and shiny; median antebasal fovea slightly smaller than lateral foveae; basal margin bordered with row of contiguous shallow impressions. Elytra together wider than long with protruding humeri; disc smooth, shiny, with some small punctures; generally four basal elytral foveae (two lateral foveae very close and sometimes merged); sutural stria entire; discal stria extending to about elytral midlength. Legs slender. Abdomen smooth, with some minute punctures; tergite I with basal striae slightly diverging, extending to about one-third of paratergal length, separated at base by about one-third of tergal width, with short and sparse setal brush between striae.

Male: Head as in Figs 23 & 26, with occiput very swollen, its anterior margin falls steeply to deep transverse sulcus. Antennae with scape short, as long as wide; pedicel slightly longer than wide; antennomeres III–VIII small and subglobose; antennomere IX transverse with protruding mesal margin; antennomere X transverse and larger than IX, with protruding mesal margin; antennomere XI ovoid, longer than wide and as long as VII-X combined. Metasternum with a large median impression occupying 2/3 of its surface; mesotibiae enlarged at middle and shallowly emarginate subapically. Abdominal tergites unmodified; all abdominal ventrites slightly flattened at middle. Aedeagus (Fig. 17) 0.28-0.29 mm long; dorsal plate elongate with sides sinuate and dorsal strips long

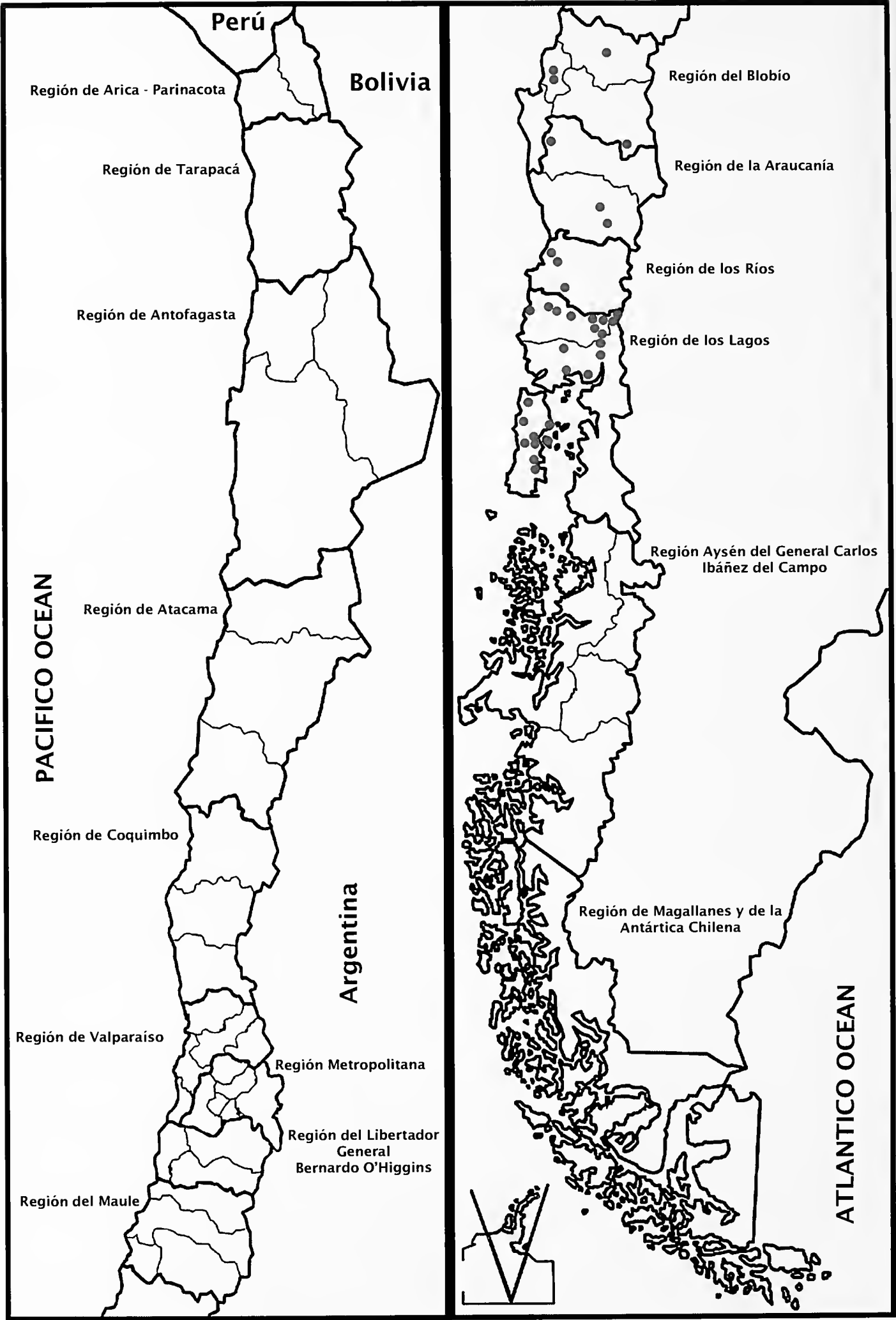


Fig. 32. Distribution map of *Achilia larvata* based on examined material.

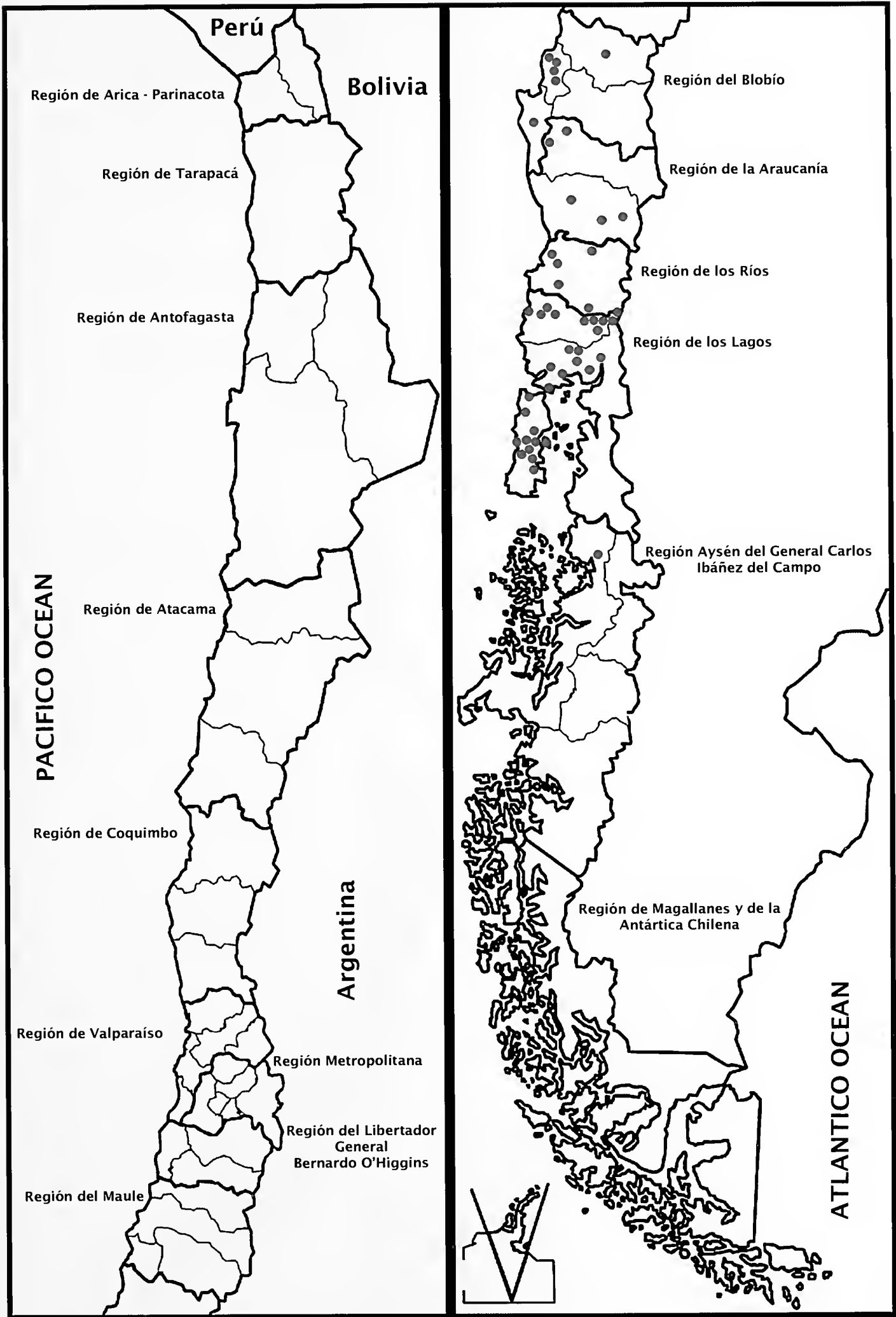


Fig. 33. Distribution map of *Achilia bifossifrons* based on examined material.

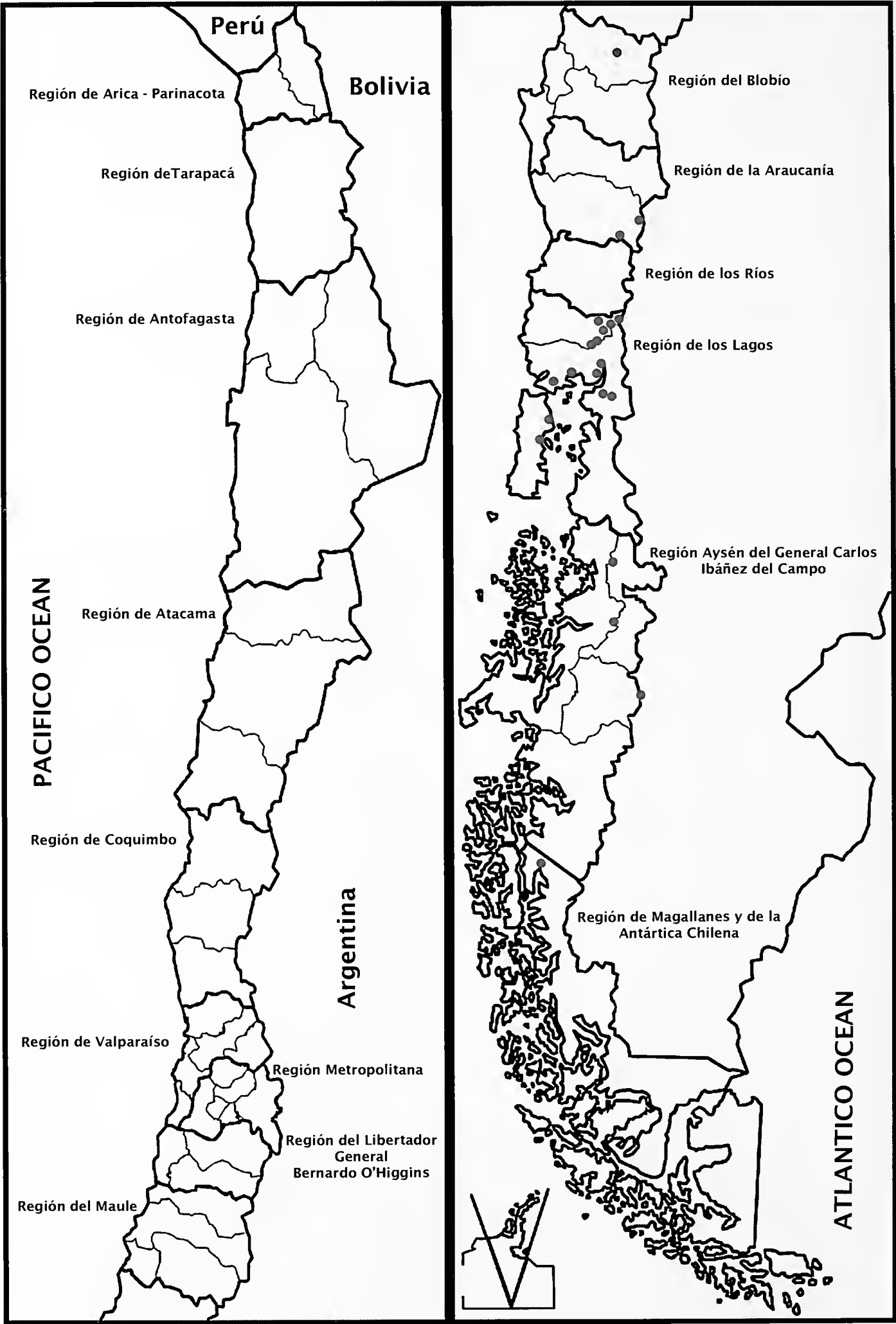


Fig. 34. Distribution map of *Achilia lobifera*. (Red dots: material examined, green dot: literature data).

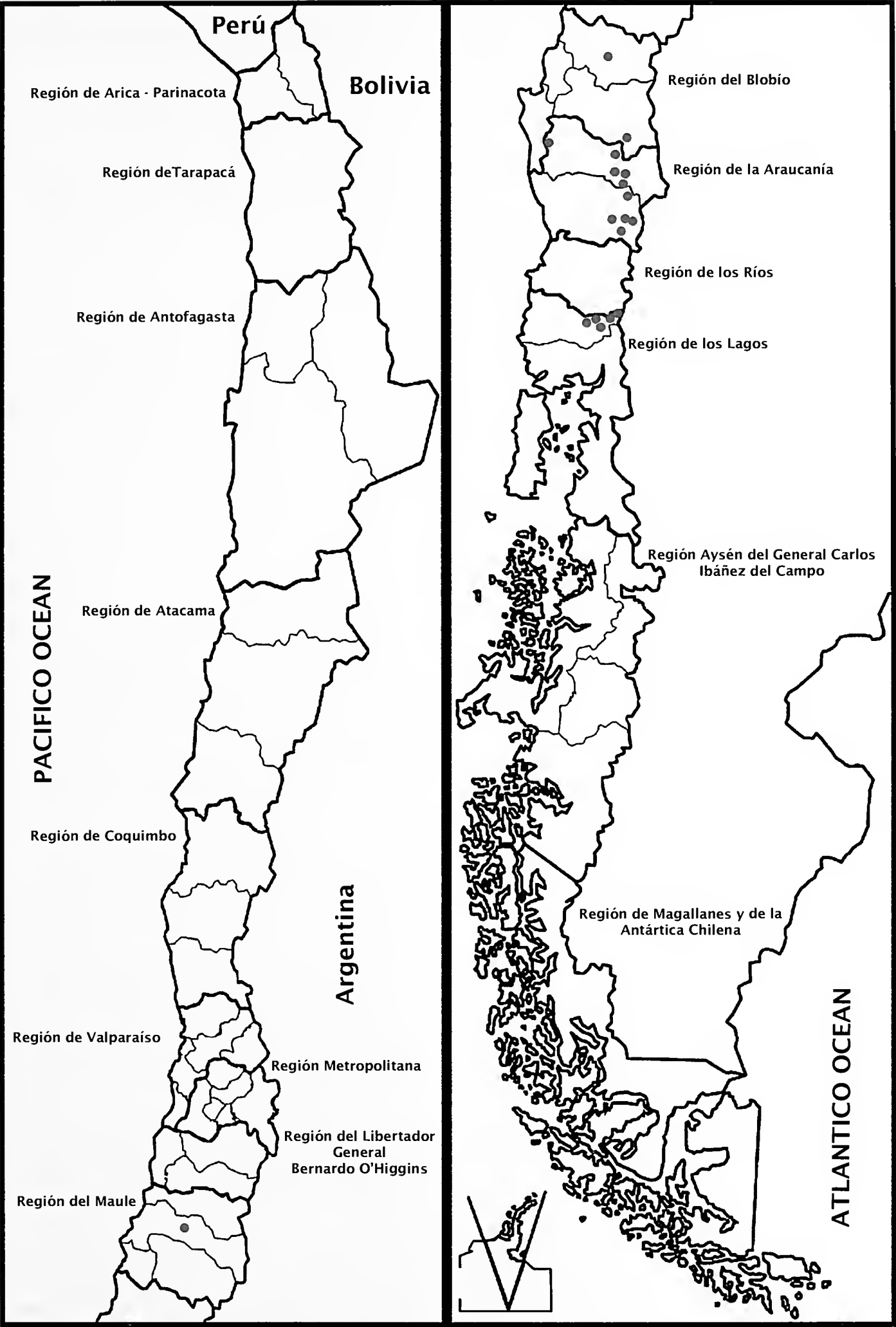


Fig. 35. Distribution map of *Achilia antennalis* (excluding Argentina) based on examined material.

and divergent; copulatory pieces consisting of pair of long sclerites curved apically. Parameres with middle seta on distinct lobe, that seta thin, reduced compared to that of the other species treated here; tips broad, recurved posteriorly.

Female: Similar to male except: head with occiput barely swollen; metasternum convex; abdominal ventrites not flattened at middle; mesotibiae unmodified.

Collecting data: Collected from September to April, mainly in *Nothofagus-Araucaria* forest and secondary and disturbed Valdivian rainforest at elevations ranging from sea level up to about 800 m. Most specimens came from sifted samples of leaf and log litter, moss on forest floor and trees, dead trunks, vegetational debris, and bracket fungi, but also by flight intercept (window) traps, screen sweeping, and car traps.

Distribution: *Achilia bifossifrons* is distributed in Central Chile from Aysén northward to Ñuble provinces (Fig. 33).

Comments: Reitter (1883) described *A. bifossifrons* based on what he thought was a unique female from Valdivia. However the description is definitely that of a male, so we recognized the only male we found in Raffray's collection as the holotype of this species, and labelled it accordingly.

Achilia lobifera group

Jeannel (1962: 397, 405) characterized this group as follows: elytra with 3 basal foveae; basal striae of abdominal tergite I separated by 1/3 of tergal width; head of male with high and narrow frontal protuberance bordered by two pits with marginal denticulations; male antennomere IV lobed; internal sac of aedeagus forming "bouquet" of spines. The group consists in *A. antennalis* Jeannel, 1962 and *A. lobifera* Jeannel, 1962.

Achilia lobifera Jeannel, 1962

Figs 13, 18, 27, 29, 34

Achilia lobifera Jeannel, 1962: 405, figs 153 (habitus), 154 (aedeagus).

Type material (43 ex.): SOUTHERN CHILE: Región Magallanes y de la Antártica Chilena: Última Esperanza prov.: MHNS; 1 ♂ (holotype of *Achilia lobifera* n° 1678); Puerto Eden; 04.XII.1958; G. Kuschel. – MNHN; 2 ♀ (paratypes of *A. lobifera*); Wellington Island, Puerto Eden; 49° 09' S; 02.XII.1958; G. Kuschel; *Nothofagus betuloides* forest. – MNHN; 15 ♂ and 14 ♀ (paratypes of *A. lobifera*); same data; 04.XII.1958; G. Kuschel. – MNHN; 2 ♂ and 4 ♀ (paratypes of *A. lobifera*); same data; 06.XII.1958. – MNHN; 1 ♂ and 4 ♀ (paratypes of *A. lobifera*); Wellington Island, Puerto Eden, Carlos Islet.

Additional material (371 ex.): See Appendix 1.

Description: Body 1.30-1.45 mm long, reddish with darker head and abdomen, with yellowish maxillary palpi. Pubescence decumbent with dense and long setae, sparser on head and pronotum. Head wider than long; surface smooth, shiny, with some minute punctures; vertexal foveae shallow and large; eyes protruding, longer than convex temples. Pronotum wider than long and wider than head, with maximal width on anterior half; posterior portion of lateral outlines sinuate; disc convex, smooth and shiny; median antebasal fovea smaller than lateral foveae; basal margin bordered with row of contiguous shallow impressions. Elytra together wider than long with very protruding humeri; disc smooth, shiny, with some minute punctures; four basal elytral foveae (two lateral foveae very close); sutural stria entire; discal stria extending to about elytral midlength. Legs slender. Abdomen smooth, with some minute punctures; tergite I with basal striae subparallel and very short, extending to less than 1/6 paratergal length, separated at base by more than one-third of tergal width, with short and sparse setal brush between striae.

Male: Head as in Figs 27 and 29. Antennae (Fig. 13) with scape longer than wide; pedicel wider than long; antennomere III strongly transverse; antennomere IV very big, longer than wide, flattened, with medial margin markedly enlarged and projecting downward, dorsal surface convex and covered with numerous large bristles; antennomere V wider than long; antennomere VI slightly longer than wide, antennomere VII distinctly longer than wide; antennomere VIII slightly wider than long; antennomere IX slightly wider than long; antennomere X distinctly wider than long; antennomere XI distinctly longer than wide, as long as VIII-X combined. Metasternum bearing large median sulcus with pubescent sides; mesotibiae forming stout subapical spur. Abdominal tergites and ventrites unmodified. Aedeagus (Fig. 18) 0.28-0.29 mm long; dorsal plate large with sides sinuate, dorsal stripes long and divergent; copulatory pieces consisting of pair of large sclerites apically enlarged and laterally ending in spine. Parameres with middle seta on distinct lobe, that seta very stout; tips broad and recurved posteriorly.

Female: Similar to male except: head with occiput only slightly swollen, frontal region flattened with slightly convergent sides and impressed vertexal sulcus; antennae unmodified, with antennomeres III to V longer than wide; metasternum convex; mesotibiae unmodified.

Collecting data: Collected from December to February in *Nothofagus* forest, temperate rainforest, mixed *Fitzroya cupressoides* forest, sclerophyll rainforest, Valdivian rainforest, and also scrub intergrading into sclerophyll rainforest at elevations ranging from sea level up to about 1000 m. Most specimens came from sifted samples of moss on logs, forest floor, tree trunks,

and rocks, from vegetational debris, dead wood and branches, but also by flight intercept (window) and car traps.

Distribution: *Achilia lobifera* is distributed in Southern and Central Chile from Última Esperanza northward to Cautín provinces (Fig. 34). Mentioned also by Jeannel (1962: 407) from Ñuble prov.: Chillán Cordillera, 36° 54' S, 2 ♂ and 3 ♀ (P. Germain), we could not locate these specimens and, consider this identification as doubtful.

***Achilia antennalis* Jeannel, 1962**

Figs 12, 19-20, 28, 30, 35

Achilia antennalis Jeannel, 1962: 405, 406

Type material (1 ex.): CENTRAL ARGENTINA: Neuquén prov.: MNHN; 1 ♂ (holotype of *Achilia antennalis*); Saint Martin de los Andes, Lanin reserve; about 40° S; 1000 m; III.1959; specimens wandering on the sandy shores of Lacar Lake; C. Delamare.

Additional material (124 ex.): See Appendix 1.

Description: Body 1.30-1.45 mm long, reddish with darker head and abdomen, with yellowish maxillary palpi. Pubescence decumbent with dense and long setae, sparser on head and pronotum. Head wider than long; surface smooth, shiny, with some minute punctures; vertexal foveae shallow and large; eyes protruding, longer than convex temples. Pronotum wider than long and wider than head, with maximal width on anterior half; posterior portion of lateral outlines sinuate; disc convex, smooth and shiny; median antebasal fovea smaller than lateral foveae; basal margin bordered with row of contiguous shallow impressions. Elytra together wider than long with very protruding humeri; disc smooth, shiny, with some minute punctures; four basal elytral foveae (two lateral foveae very close); sutural stria entire; discal stria extending to about elytral midlength. Legs slender. Abdomen smooth, with some minute punctures; tergite I with basal striae subparallel and very short, extending to less than 1/6 paratergal length, separated at base by more than one-third of tergal width, with short and sparse setal brush between striae.

Male: Head as in Figs 28 and 30. Antennae (Fig. 12) with scape longer than wide; pedicel slightly longer than wide; antennomere III small and transverse; antennomere IV wider than long with medial margin enlarged, anterior margin thicker than posterior, dorsal surface slightly concave and covered with numerous very little bristles, antennomeres V-X wider than long; antennomere XI distinctly longer than wide, longer than VIII-X combined. Metasternum bearing large median sulcus with pubescent sides; mesotibiae forming stout subapical spur. Abdominal tergites and ventrites unmodified.

Aedeagus (Figs 19-20) 0.28-0.29 mm long; dorsal plate large with sides sinuate; dorsal strips long and divergent; copulatory pieces consisting of pair of large sclerites that are apically enlarged and trifid, laterally ending in four tips. Parameres with middle seta on distinct lobe, that seta very stout; tips broad recurved posteriorly.

Female: Similar to male except: head with occiput only slightly swollen, frontal region flattened with slightly convergent sides and impressed vertexal sulcus; antennae unmodified, with antennomeres III as long as wide and IV-V slightly longer than wide; metasternum convex; mesotibiae unmodified.

Collecting data: Collected from December and March in *Nothofagus* forest that is sometimes with *Chusquea*, in *Saxegothea* forest with *Drimys*, and in *Araucaria araucana* forest at elevations ranging from 300 m up to about 1500 m. Most specimens came from sifted samples of leaf and log litter, but also were taken by flight intercept (window) and malaise traps. Jeannel (1962: 407) reports that specimens were collected wandering on the sandy shores of Lacar Lake (Argentina, Neuquén province).

Distribution: *Achilia antennalis* is distributed for Central Western Argentina (Neuquén province) and Central Chile from Osorno to the Maule region (Talca province) (Fig. 35).

Comments: In the original description Jeannel (1962) mentioned five males (holotype and paratypes) collected in Saint Martin de los Andes. He also stated that *A. antennalis* and *A. lobifera* have the same external and aedeagal morphology, and differ only by the shape of the male head and antennae, however, the aedeagi are really distinctive, notably in examination of the copulatory pieces (Figs 18-19).

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- Appendix 1**
- Non-type material examined for the species mentioned in the Taxonomy section
- Achilia crassicornis* Jeannel, 1962
- Additional material (2166 ex.):** SOUTHERN AND CENTRAL WESTERN ARGENTINA: Tierra del Fuego prov.: DBUC; 2 ♀; Peninsula Mitre, Bahía Tethys, 22.I.1989; S. Motta. - DBUC; 2 ♂; Peninsula Mitre, Bahía Valentina, station 38; 24.I.1989; S. Motta. - DBUC; 1 ♂ and 2 ♀; Peninsula Mitre, Río Lopez, station 40; 24.I.1989; S. Motta. - DBUC; 1 ♂; same data; 03.I.1989; S. Motta. - DBUC; 1 ♂; Peninsula Mitre, Caleta Poliearpo, station 41; 25.I.1989; S. Motta. - DBUC; 2 ♂ and 3 ♀; Ushuaia National Park; 07.I.1989; S. Motta. - DBUC; 1 ♂; Ushuaia, Río Pipo; 03.I.1989; S. Motta. - DBUC; 4 ♂ and 6 ♀; Ushuaia, Mount San Martial; 31.XII.1988; S. Motta. - DBUC; 4 ♂ and 1 ♀; Ushuaia, San Martial Glacier; 01.I.1989; S. Motta; boundary between forest and stony ground. - MHNG; 3 ♂ and 1 ♀ (sub *A. antarctica*); Ushuaia, Mount Susana; 26.III.1975; E. Hozak. - Río Negro prov.: MHNG; 1 ♂; El Bolson, Topál, nr. 24; 23.X.1961. - Neuquén prov.: MNHN; 2 ♂; Saint Martin de los Andes, Lanin reserve; about 40° S; 1000 m; 15.IV.1959; C. Delamare; specimens wandering on the sandy shores of Lacar Lake. - SOUTHERN AND CENTRAL CHILE: Región de Magallanes y de la Antártica Chilena: Antártica Chilena prov.: MHNS; 1 ♀ (mislabelled as paratype of *Achilia crassicornis antarctica* n° 1625); Navarino Island, Puerto Williams; 31.I.1957; G. Kuschel. - MHNS; 1 ♀ (mislabelled as paratype of *Achilia crassicornis crassicornis* n° 1578); Puerto Eden; 06.XII.1958; G. Kuschel. - MNHN; 3 ♂ (sub *Achilia antarctica*); Picton Island, Puerto Banner; 55° 00'S; 14.I.1959; G. Kuschel; *Nothofagus betuloides* and *Nothofagus antarctica* forest. - DBUC; 2 ♂ and 2 ♀; Picton Island, station 11; 20.I.1990; S. Motta. - MHNG; 2 ♂; Navarino Island, Puerto Williams, station 1; 55° 10'S 69° 30'W; 20 m; 26.I/02.II.1985; J. Vogel. - DBUC; 1 ♂; Lennox Island, station 13; 20.I.1990; S. Motta. - DBUC; 1 ♂; Hoste Island, station 9; 20.I.1990; S. Motta. - DBUC; 1 ♂ and 1 ♀; Hoste Island, station 10; 20.I.1990; S. Motta. - DBUC; 3 ♂ and 17 ♀; Cordillera Darwin 2, station 19; 21.I.1990; S. Motta. - Tierra del Fuego prov.: DBUC; 1 ♂; Seno Almirantazgo, station 18; 21.I.1990; S. Motta. - FMNH; 8 ♂ and 6 ♀; Bahía Inútil, Cameron; 14-16.XI.1960; L. Peña. - Magallanes prov.: NHMW; 1 ♀; Magallanes province; H. Franz. - NHMW; 17 ♂ and 40 ♀; Peninsula New Brunswick; H. Franz. - MNHN; 6 ♂ and 5 ♀; Peninsula Brunswick, Río Tres Brazos, near Punta Arenas; 53° 18'S; 19.I.1957; G. Kuschel. - MHNS; 1 ♂ (mislabelled as paratype of *Achilia crassicornis crassicornis* n° 1620); same data; G. Kuschel. - MNHN; 1 ♀; Peninsula Brunswick, Chozillo Larques, near Punta Arenas; 12.III.1960; T. Cekalovic. - MNHN; 1 ♂; Peninsula Brunswick, Cueva Millodon, near Punta Arenas; XII.1960; T. Cekalovic. - MNHN; 1 ♂ and 1 ♀; Peninsula Brunswick, Río El Ganso; 12.II.1961; T. Cekalovic. - MNHN; 1 ♀; same data; T. Cekalovic. - MNHN; 3 ♂ and 1 ♀; Peninsula Brunswick, Río Caleta; 26.II.1961; T. Cekalovic. - MHNG; 1 ♂ and 6 ♀; Peninsula Brunswick, Parillar National Reserve, station 44b; 300 m; 17.I.1991; D. Burekhardt; *Nothofagus betuloides* forest. - MHNG; 1 ♂; Peninsula Brunswick, Fuerte Bulnes, station 45a; 10 m; 17.I.1991; D. Burekhardt; *Nothofagus betuloides* forest. - DBUC; 1 ♂ and 1 ♀; same data; D. Burekhardt. - DBUC; 5 ♂ and 9 ♀; Peninsula Brunswick, Cabo Froward, station 26; 30.I.1990; S. Motta. - DBUC; 1 ♂ and 2 ♀; Clarence Island, station 28; 30.I.1990; S. Motta. - Última Esperanza prov.: MNHN; 7 ♂ and 6 ♀; Río Rubens; 52° 00'S; 18.I.1957; G. Kuschel. - MHNS; 1 ♂ (mislabelled as paratype of *Achilia crassicornis crassicornis* n° 1608); same data; G. Kuschel. - Región Aysén: General Carrera prov.: MNHN; 3 ♂ and 5 ♀; Chieo, east end of Buenos Aires Lake; 17.I.1956; G. Kuschel. - MNHN; 9 ♂ and 6 ♀; Río Murta, NW end of Buenos Aires Lake; 46° 28'S; 25.I.1956; G. Kuschel; forest. - MHNS; 1 ♂ (mislabelled as paratype of *Achilia crassicornis crassicornis* n° 1595); Río Murta; 25.I.1956; G. Kuschel. - Coyhaique prov.: MHNG; 1 ♂; environs of Coyhaique; H. Franz. - NHMW; 1 ♂; same data; H. Franz. - MHNG; 1 ♂; 40 km SW Balmaceda, Cerro Castillo Natural Reserve; 1100 m; 02-27.I.1995; S. & J. Peck; FIT dry open beech forest. - Aysén prov.: MHNG; 25 ♂ and 6 ♀; 30 km N Puyuhapi, station 107; 100 m; 29.I.1985; S. & J. Peck. - FMNH; 6 ♂ and 1 ♀; same data; S. & J. Peck. - DBUC; 1 ♂ and 1 ♀, same data, S. & J. Peck. - FMNH; 37 ♂ and 29 ♀; Frío Lake, Coyhaique; 20-23.I.1961; L. Peña. - Región Los Lagos: Chiloé prov.: MNHN; 1 ♂ and 1 ♀ (sub *A. tumidifrons*); Cerros de San Pedro; 42° 20'S; 520 m; 10.XI.1958; G. Kuschel; wet forest. - MNHN; 1 ♂ and 1 ♀ (sub *A. tumidifrons*); same data; G. Kuschel. - MHNS; 1 ♂ (mislabelled as paratype of *Achilia crassicornis crassicornis* n° 1586); San Pedro; 10.XI.1958; G. Kuschel. - MHNG; 2 ♂ and 2 ♀; Chiloé National Park, Cucao, 30 km SW Castro, station 29a; 30 m; 04-06.I.1991; M. Agosti & D. Burekhardt; temperate rainforest. - MHNG; 1 ♂ and 1 ♀; Chiloé National Park, near Cucao, 30 km SW Castro, station 34b; 42° 37'S 74° 08'W; 10-70 m; 28.XII.1992/01.I.1993; D. Burekhardt; sifting of moss on forest floor trees and dead trunks and vegetational debris. - MHNG; 1 ♂ and 3 ♀; Chiloé National Park, Rancho Grande, near Cucao, station 35b; 42° 33'S 74° 02'W; 250-400 m; 29.XII.1992; D. Burekhardt; sifting of moss on forest floor trees and vegetational debris. - MHNG; 5 ♂ and 13 ♀; Chiloé Island, 8 km of Aneud, station 110; 01.II.1985; S. & J. Peck; forest remnants litter. - FMNH; 1 ♂ and 3 ♀; same data; S. & J. Peck. - DBUC; 1 ♂ and 1 ♀; same data; S. & J. Peck. - FMNH (FMHD #2002-068); 50 ♂ and 82 ♀; 11 km W of Quemci (11 km E Hwy 5); 42° 10.40'S 73° 35.73'W; 140 m; 10.XII.2002; A. Solodovnikov & A. Newton 1060; valdivian rainforest remnant w/thick bamboo understory; berlese, leaf & log litter. - Llanquihue prov.: MNHN; 1 ♂; Frutillar; 41° 08'S; 20.IX.1954; G. Kuschel. - MHNG; 13 ♂ and 6 ♀; Alerce Andino National Park, above Laguna Chaiquenes, station 37; 41° 40'S 72° 35'W; 350-650 m; 04.I.1993; D. Burekhardt; mixed *Fitzroya cupressoides* forest with

thick moss cover inside, sifting of moss on floor and tree trunks and vegetational debris. – FMNH (FMHD #97-28); 1 ♂; Alerce Andino National Park, near Sargazo entrance, 11.4 km from Correntoso; 41° 30'S 72° 37'W; 350 m; 19.I.1997; A. Newton & M. Thayer 998; valdivian rainforest, berlese, leaf & log litter. – FMNH (FMHD #97-30); 2 ♀; Alerce Andino National Park, N side Laguna Sargazo; 41° 30'S 72° 36'W; 400 m; 21.I.1997; A. Newton & M. Thayer 1000; *Fitzroya eupressoides* w/valdivian rainforest understory steep slope, berlese, leaf & log litter. – UNHC; 3 ♂; Lago Chapo, 13.5 km E Correntoso, site 656; 310 m; 16-27.XII.1982; A. Newton & M. Thayer; valdivian rainforest, flight intercept (windows) trap. – FMNH (FMHD #97-16); 4 ♂ and 6 ♀; Lago Chapo, near SE end, km 9.9 on road from Rollizo; 41° 30.63'S 72° 23.98'W; 385 m; 04.I.1997; A. Newton & M. Thayer 989; valdivian rainforest on steep slope, berlese, leaf & log litter. – FMNH (FMHD #97-26); 9 ♂ and 23 ♀; Lago Chapo, 1.2 km N of NW end; 41° 25'S 72° 35'W; 265 m; 19.I.1997; A. Newton & M. Thayer 996; small secondary *Nothofagus dombeyi* w/valdivian rainforest understory, berlese, leaf & log litter. – FMNH (FMHD #85-938, #85-54); 1 ♂; Vicente Perez Rosales National Park, Salto Petrohué; 150 m; 23.XII.1984; S. & J. Peck; mixed forest litter, berlese. – FMNH (FMHD #85-995, #85-112); 1 ♀; Vicente Perez National Park, Salto Petrohué; 150 m; 04.II.1985; S. & J. Peck; mixed forest litter, berlese. – FMNH (FMHD #97-8); 1 ♂; Vicente Perez Rosales National Park, 9.2 km NE Ensenada, on road to Petrohué; 41° 10.20'S 72° 27.10'W; 125 m; 02-28.I.1997; A. Newton & M. Thayer 987; valdivian rainforest w/ *Nothofagus* spp., flight intercept trap. – FMNH (FMHD #97-11); 5 ♂ and 1 ♀; Vicente Perez Rosales National Park, SW slope Vn Osorno, km 10.1 to La Burbuja; 41° 08.30'S 72° 32.15'W; 925 m; 03-27.I.1997; A. Newton & M. Thayer 988; *Nothofagus dombeyi* & *Podocarpus nubigena* w/valdivian rainforest understory, flight intercept trap. – FMNH (FMHD #97-12); 1 ♂; same data; A. Newton & M. Thayer 988; *Nothofagus dombeyi* & *Podocarpus nubigena* w/valdivian rainforest understory, carrion trap (squid). – FMNH (FMHD #97-13); 10 ♀; same data; 03.I.1997; A. Newton & M. Thayer 988; low *Nothofagus dombeyi* & *Podocarpus nubigena* w/valdivian rainforest understory, berlese, leaf & log litter. – FMNH (FMHD #97-35); 20 ♂ and 75 ♀; Vicente Perez Rosales National Park, SW slope Vn Osorno, km 11 to La Burbuja; 41° 07.91'S 72° 32.16'W; 1065 m; 27.I.1997; A. Newton & M. Thayer 1005; low *Nothofagus dombeyi* w/mixed understory, berlese, leaf & log litter. – FMNH (FMHD #97-37); 1 ♂; Vicente Perez Rosales National Park, SW slope Vn Osorno, km 6 to La Burbuja; 41° 09.08'S 72° 30.15'W; 925 m; 27.I.1997; A. Newton & M. Thayer 1006; low *Nothofagus dombeyi* on lava w/shrubby understory, berlese, litter under leaves, mosses & lichens. – FMNH (FMHD #2002-80); 7 ♂ and 29 ♀; Vicente Perez Rosales National Park, SW slope Voleán Osorno, ea km 10 to La Burbuja; 41° 07.9'S 72° 32'W; 1090 m; 15.XII.2002; A. Solodovnikov 1065; *Nothofagus dombeyi* w/bamboo shrub understory, berlese, leaf & log litter. – FMNH (FMHD #2002-81); 7 ♂ and 74 ♀; Vicente Perez Rosales National Park, SW slope Voleán Osorno, km 10 to La Burbuja; 41° 08.33'S 72° 32.16'W; 910 m; 15.XII.2002; M. Thayer & A. Solodovnikov 1066; *Nothofagus dombeyi* w/mixed understory, berlese, leaf & log litter. – FMNH (FMHD #2002-085); 1 ♂; Ensenada, Las Cascadas road, 0.9 km N of La Burbuja; 41° 11.27'S 72° 32.6'W; 80 m; 16.XII.2002; M. Chani; *Nothofagus dombeyi*, mixed hardwoods, berlese, litter. – Osorno prov.: MHNG; 3 ♂ and 1 ♀; Puyehue National Park, Antillanca Road; 500-1000 m; 18-20.XII.1984; S. & J. Peck; car netting. – MHNG; 4 ♂; Puyehue National Park, Antillanca Road; 600-1000 m; 20.XII.1984; S. & J. Peck, car netting. – UNHC; 4 ♂ and 3 ♀; Puyehue National Park, Antillanca road, site 660; 845 m; 18-24.XII.1982; A. Newton & M. Thayer; *Nothofagus-Saxegothea* forest, berlese, leaf & log litter, forest floor. – FMNH; 21 ♂ and 24 ♀; same data; A. Newton & M. Thayer. – UNHC; 1 ♂; Puyehue National Park, Antillanca road, trap site 658; 925 m; 18-25.XII.1982; A. Newton & M. Thayer; *Nothofagus pumilio* forest, berlese, leaf & log litter, forest floor. – FMNH; 3 ♂ and 12 ♀; same data; A. Newton & M. Thayer. – UNHC; 3 ♂; Puyehue National Park, Antillanca road, site 659; 720 m; 18-24.XII.1982; A. Newton & M. Thayer; *Nothofagus* spp. forest, flight intercept (windows) trap. – FMNH (FMHD #97-1); 10 ♂; Puyehue National Park, Antillanca Road, approaching ski center; 40° 46.85'S 72° 13.03'W; 980 m; 01.I-01.II.1997; A. Newton & M. Thayer 986; open *Nothofagus pumilio* forest w/*Chusquea*, flight intercept trap.

– FMNH (FMHD #97-3); 29 ♂ and 54 ♀; same locality; 01.I.1997; A. Newton & M. Thayer 986; open *Nothofagus pumilio* forest w/dense *Chusquea*, berlese, leaf & log litter. – UNHC; 1 ♂; Antillanea; 1200 m; 16.II.1988; L. Masner; treelines *Nothofagus*. – FMNH (FMHD #2002-88); 4 ♂; Puyehue National Park, Ruta 215; near Laguna Las Mellizas; 40° 40.8'S 71° 59.4'W; 1000 m; 19.XII.2002; A. Newton & M. Thayer 1070; *Nothofagus pumilio* forest w/ dense bamboo understory, berlese, wet debris in large stream. – FMNH (FMHD #2002-90); 30 ♂ and 30 ♀; Puyehue National Park, Ruta 215; km 4.5 of Aduana station; 40° 40.23'S 72° 05.21'W; 580 m; 19.XII.2002; A. Newton, M. Thayer, D. J. Clarke & M. Chani 1071; valdivian rainforest, berlese, leaf & log litter. – MHNG; 13 ♂ and 11 ♀; Puyehue National Park, road Aguas Calientes-Antillanea, station 19b; 40° 45'S 72° 15-20'W; 750-850 m; 30.XI/01.XII.1992; D. Burekhardt; sifting of moss on tree trunks and forest floor and vegetational debris. – MHNG; 1 ♂; Puyehue National Park, Aguas Calientes, station 20 b; 40° 40'S 72° 20'W; 450-600 m; 01-03.XII.1992; D. Burekhardt; sifting of moss on dead tree trunks, branches and rocks and vegetational debris. – MHNG; 1 ♂ and 1 ♀; Puyehue National Park, Aguas Calientes, station 25a; 400-500 m; 31.XII.1990/01.I.1991; M. Agosti & D. Burekhardt. – MHNG; 2 ♂ and 2 ♀; Puyehue National Park, Aguas Calientes to Antillanca, station 27a; 1000 m; 02.I.1991; M. Agosti & D. Burekhardt. – DBUC; 1 ♂; same data; M. Agosti & D. Burekhardt. – MHNG; 1 ♂ and 3 ♀; Puyehue National Park, Aguas Calientes to Antillanea, station 28a; 800 m; 02.I.1991; M. Agosti & D. Burekhardt. – FMNH (FMHD #96-246); 1 ♂; Puyehue National Park, Antillanea road, 7.2 km above Aguas Calientes, 40° 45.55'S 72° 17.82'W; 660 m; 29.XII.1996; A. Newton & M. Thayer 982; valdivian rainforest w/ *Saxegothea* dominant, dense *Chusquea*, berlese, leaf & log litter. – FMNH (FMHD #2002-087); 185 ♂ and 216 ♀; Puyehue National Park, W side Paso Cardenal Samoré; 40° 42.65'S 71° 56.66'W; 1305 m; 17.XII.2002; A. Newton, M. Thayer & A. Solodovnikov 1069; timberline *Nothofagus pumilio* forest with snow patches, berlese, leaf & log litter. – FMNH; 1 ♂; same data; A. Newton 1069; timberline, *Nothofagus pumilio* forest with snow patches, on small orange gilled mushrooms. – MHNG; 1 ♂; same data; A. Newton 1069. – DBUC; 1 ♂; same data; A. Newton 1069. – UNHC; 1 ♂; Puyehue National Park, 4.1 km E Antieura, trap site 662; 430 m; 19-26.XII.1982; A. Newton & M. Thayer; valdivian rainforest, screen sweeping. – FMNH; 1 ♂; same data; A. Newton & M. Thayer. – FMNH; 5 ♂; same locality; 19-26.XII.1982; A. Newton & M. Thayer; valdivian rainforest, vouchers associated with larvae, berlese, leaf & log litter, forest floor. – FMNH (FMHD #96-250); 2 ♂; Puyehue National Park, 4 km E Antieura; 40° 39.73'S 72° 08.10'W; 460 m; 30.XII.1996/30.I.1997; A. Newton & M. Thayer 985-1; valdivian rainforest w/large, *Saxegothea*, flight intercept trap. – FMNH (FMHD #97-4); same locality; 01-30.I.1997; A. Newton & M. Thayer; valdivian rainforest w/large, *Saxegothea*, flight intercept trap. – FMNH (FMHD #97-5); 2 ♂ and 1 ♀; same data; A. Newton & M. Thayer 985-3; valdivian rainforest w/large, *Saxegothea*, flight intercept trap. – FMNH (FMHD #97-39); 4 ♂; same locality; 30.I.1997; A. Newton & M. Thayer 985-3; valdivian rainforest w/large, *Saxegothea* berlese, leaf & log litter. – FMNH (FMHD #97-41); 2 ♂; same data; A. Newton & M. Thayer 985-1; valdivian rainforest w/large, *Saxegothea*, berlese, leaf & log litter. – FMNH (FMHD #97-4); 3 ♂; same data; A. Newton & M. Thayer 985-2; valdivian rainforest w/large, *Saxegothea*, berlese, leaf & log litter. – UNHC; 1 ♂; Puyehue National Park, Voleán Casablanca; 1100-1130 m; 20.XII.1982; A. Newton & M. Thayer; *Nothofagus pumilio-antaretica* forest with *Drinys*, berlese, leaf & log litter, forest floor. – FMNH; 34 ♂ and 100 ♀; same data; A. Newton & M. Thayer. – UNHC; 1 ♂; Puyehue National Park, Voleán Casa Blanca, trap site 667; 1270 m; 20-25.XII.1982; A. Newton & M. Thayer; treeline *Nothofagus* forest, pan trap. – FMNH (FMHD #2002-81); 101 ♂ and 180 ♀; Vicente Perez Rosales National Park, SW slope Voleán Osorno, road to Ref. La Pieada; 41° 03.25'S 72° 30.18'W; 660 m; 16.XII.2002; A. Solodovnikov, A. Newton & M. Thayer 1067; *Nothofagus dombeyi* w/ conifers dense *Chusquea* bamboo understory, flat area, berlese, leaf & log litter. – FMNH (FMHD #2002-81); 20 ♂ and 43 ♀; Vicente Perez Rosales National Park, SW slope Voleán Osorno, road to Ref. La Pieada; 41° 01.05'S 72° 32.90'W; 430 m; 16.XII.2002; A. Newton, A. Solodovnikov & M. Chani 1068; *Nothofagus dombeyi* w/ conifers, berlese, leaf & log litter. – Región Araucanía: Cautín prov.: MHNG; 2

♂; Villarica National Park, Volcán Villarica, 10 km S Pucón; 900 m; 15.XII.1984/10.II.1985, S. & J. Peck; *Nothofagus* grove on ash. – UNHC; 1 ♂; Volcán Villarica, site 654; 1120 m; 15-29.XII.1982; A. Newton & M. Thayer; *Nothofagus dombeyi*-*Saxegothea* forest with *Drimys*, flight intercept (windows) trap. – FMNH (FMHD #96-237); 1 ♂; Villarica National Park, Volcán Villarica, road to sky center; 39° 22.48'S 71° 58.30'W; 1180 m; 26.XII.1996/03.II.1997; A. Newton & M. Thayer 980; *Nothofagus dombeyi* forest w/*Chusquea*, flight intercept trap. – FMNH (FMHD #96-239); 12 ♂ and 22 ♀; same locality; 26.XII.1996; A. Newton & M. Thayer 980; *Nothofagus dombeyi* forest w/*Chusquea*, berlese, leaf & log litter. – FMNH (FMHD #96-241); 1 ♂; Villarica National Park, Volcán Villarica, road to sky center; 39° 23.27'S 71° 57.82'W; 1390 m; 27.XII.1996/03.II.1997; A. Newton & M. Thayer 981; *Nothofagus pumilio* forest, flight intercept trap. – FMNH (FMHD #96-242); 1 ♂; same data; A. Newton & M. Thayer 981; stunted *Nothofagus pumilio* forest, carrion trap (squid). – MHNG; 1 ♂; same data; A. Newton & M. Thayer 981. – FMNH (FMHD #96-243); 2 ♂ and 6 ♀; same locality; 27.XII.1996; A. Newton & M. Thayer 981; stunted *Nothofagus pumilio* forest, berlese, leaf & log litter. – MHNG; 1 ♂; same data; A. Newton & M. Thayer 981. – MHNG; 8 ♂ and 14 ♀; Huerquehue National Park, station 16a; 800-900 m; 22-24.XII.1980; M. Agosti & D. Burckhardt; forest litter. – DBUC; 1 ♂ and 1 ♀; same data; M. Agosti & D. Burckhardt. – MHNG; 1 ♂ and 3 ♀; Conguillío National Park, station 12a; 950 m; 19-21.XII.1990; M. Agosti & D. Burckhardt; forest litter. – MHNG; 2 ♂ and 1 ♀; Conguillío National Park, Playa Linda, station 13a; 1150 m; 19-20.XII.1990; M. Agosti & D. Burckhardt; forest litter. – DBUC; 1 ♂ and 1 ♀; same data; M. Agosti & D. Burckhardt. – MHNG; 3 ♂ and 2 ♀; Conguillío National Park, Playa Linda, station 13b; 1150 m; 19-20.XII.1990; M. Agosti & D. Burckhardt; *Nothofagus* ant. forest. – FMNH (FMHD #96-226); 1 ♂; Conguillío National Park, 11.1 km SE Laguna Captrén guard sta.; 38° 40.05'S 71° 37.21'W; 1080 m; 23.XII.1996/05.II.1997; A. Newton & M. Thayer 976; *Nothofagus obliqua* & *alpina*, dense *Chusquea* understory, flight intercept trap – FMNH (FMHD #96-228); 7 ♂ and 21 ♀; same locality; 23.XII.1996; A. Newton & M. Thayer 976; *Nothofagus obliqua* & *alpina*, dense *Chusquea* understory, berlese, leaf & log litter. – Malleco prov.: MHNG; 5 ♂; 40 km W CuraCautín; 1500 m; 12.XII.1984/16.II.1985; S. & J. Peck; *Nothofagus* and *Araucaria* forest, malaise. – MHNG; 2 ♂; environs of Malalcahuello; H. Franz. – MSNG; 1 ♂; Conguillío; 19.IV.1987; S. Gonzales. – FMNH (FMHD #97-46); 24 ♂ and 87 ♀; Conguillío National Park, 4.9 km of N entrance (road from CuraCautín); 38° 37.84'S 71° 43.31'W; 1210 m; 05.II.1997; A. Newton & M. Thayer 1009; *Araucaria-Nothofagus* forest on ash/lava; berlese, litter under *Araucaria araucana*. – Región Bío Bío: Ñuble prov.: MHNG; 1 ♂ and 4 ♀; 10 km W Termas de Chillán, station 5a; 1250 m; 12-13.XII.1990; M. Agosti & D. Burckhardt; *Nothofagus* forest litter. – UNHC; 2 ♂; Las Trancas, 19.5 km ESE Recinto, site 647; 1250 m; 10.XII.1982/03.I.1983; A. Newton & M. Thayer; *Nothofagus* forest, flight intercept (windows) trap.

Achilia larvata (Reitter, 1885)

Additional material (1284 ex.): FMNH (Orlando Park Psclaphidae collection, ex F. C. Fletcher collection); 2 ♀; Chile. – CENTRAL CHILI: Región Los Lagos: Chiloé prov.: MHNS; 2 ♀ (mislabelled paratypes of *Achilia tumidifrons* n° 1640 and 1642); Chepu; 03.X.1958; G. Kuschel. – MHNS; 1 ♂ (mislabelled paratypes of *Achilia tumidifrons* n° 1644); Chepu; 04.X.1958; G. Kuschel. – MHNS; 3 ♀ (mislabelled paratypes of *Achilia tumidifrons* n° 1633, 1635 and 1639); Chepu; 15.X.1958; G. Kuschel. – MHNG; 7 ♂ and 21 ♀; Chiloé Island, Huillínco Lake; 31.I.1983; T. Cekalovic. – DBUC; 1 ♂ and 6 ♀, same data; T. Cekalovic. – MSNG; 1 ♂; same locality; TC-278; 21.II.1991, T. Cekalovic. – MSNG; 1 ♀ and 18 ♀; Chiloé Island, 1 km W of Huillínco Lake; TC-564; 24.I.1998; T. Cekalovic. – MHNG; 1 ♀; Chiloé Island, Río Pudeto; 28.II.1972; T. Cekalovic. – MHNG; 2 ♀; same locality; 27.I.1983; T. Cekalovic. – DBUC; 1 ♂ and 1 ♀; same data; T. Cekalovic. – MSNG; 1 ♂ and 1 ♀; same locality; SyTC-226; 21.II.1989; S. & T. Cekalovic. – UNHC; 1 ♂; Chiloé Island, 2 km N Puente Río Pudeto; 20.I.2000; T. Cekalovic. – MHNG; 1 ♀; San Pedro; 22.II.1976; T. Cekalovic. – FMNH (FMHD #97-21); 8 ♂ and 9 ♀; Puente La Caldera,

9.8 km E of Cucao; 42° 39.96'S 74° 00.70'W; 10 m; 14.I.1997; A. Newton & M. Thayer 991; valdivian rainforest, berlese, leaf & log litter. – MSNG; 20 ♂ and 17 ♀; Chiloé Island, Puente La Caldera; TC-466; 15.II.1996, T. Cekalovic. – MSNG; 2 ♂; same locality; TC-524; 18.II.1997; T. Cekalovic. – MSNG; 1 ♂; Chiloé Island, Chepu; TC-275; 19.II.1991; T. Cekalovic. – MSNG; 2 ♂ and 2 ♀; same locality; TC-580; 09.II.1999; T. Cekalovic. – MSNG; 14 ♀; same locality; TC-610; 20.I.2000; T. Cekalovic. – MSNG; 12 ♂ and 2 ♀; same locality; TC-624; 26.I.2000, T. Cekalovic. – MSNG; 6 ♂ and 3 ♀; same locality; TC-625; 26.I.2000, T. Cekalovic. – MSNG; 1 ♂ and 1 ♀; Chiloé Island, Estero Tablin; TC-609; 19.I.2000, T. Cekalovic. – MSNG; 1 ♀; Chiloé Island, 1 km N of Puente Notuco; TC-528; 20.II.1997; T. Cekalovic. – MSNG; 4 ♀; Chiloé Island, Puente Milildeo; TC-471; 15.II.1995; T. Cekalovic. – MSNG; 1 ♀; Chiloé Island, San Juan de Chadmo; TC-555; 18.I.1998, T. Cekalovic. – MSNG; 2 ♂; Chiloé Island, 5 km SW Chonchi; 14.I.1999, T. Cekalovic. – MSNG; 4 ♂ and 4 ♀; same locality; TC-560; 21.I.1998; T. Cekalovic. – MSNG; 11 ♂ and 19 ♀; Chiloé Island, Estero Llicaldad; TC-608; 19.I.2000; T. Cekalovic. – MSNG; 1 ♀; Quinchao Island, Laguna Pulul; TC-615; 22.I.2000; T. Cekalovic. – Llanquihue prov.: MHNG; 1 ♂ and 5 ♀; La Arena, 45 km SE Puerto Montt; 100 m; 25.XII.1984; S. & J. Peck. – MHNG; 3 ♀; Petrohué; 30.I.1979; A. De Chambrier. – FMNH (FMHD #85-995, #85-112); 2 ♂; Vicente Perez National Park, Salto Petrohué; 150 m; 04.II.1985; S. & J. Peck; mixed forest litter, berlese. – FMNH (FMHD #85-947, #85-63); 4 ♀; Lenca, 45 km SE Puerto Montt; 100 m; 25.XII.1984; S. & J. Peck; forest remnant, leaf stick litter, berlese. – MHNS; 1 ♂ and 1 ♀ (mislabelled paratypes of *Achilia globiceps* n° 1647 and 1657); Frutillar; 20.IX.1954; G. Kuschel. – MHNG; 1 ♂ and 1 ♀; Frutillar Bajo, Universidad Chile Forest Reserve; 100 m; 22.XII.1984/02.II.1985; S. & J. Peck; FIT ravine mixed forest. – DBUC; 1 ♂ and 1 ♀, same data; S. & J. Peck. – FMNH (FMHD #2002-085); 3 ♀; Ensenada, Las Cascadas road, 0.9 km N of La Burbuja; 41° 11.27'S 72° 32.6'W; 80 m; 16.XII.2002; M. Chani; *Nothofagus dombeyi*, mixed hardwoods, berlese, litter. – FMNH (FMHD #97-38); 3 ♂ and 7 ♀; Vicente Perez Rosales National Park, SW slope Vn Osorno, km 4 to La Burbuja; 41° 09.95'S 72° 30.80'W; 310 m; 27.I.1997; A. Newton & M. Thayer 1007; secondary valdivian rainforest w/*Nothofagus dombeyi*-*Eucryphia cordifolia* berlese, leaf & log. – Osorno prov.: MHNG; 3 ♂; environs of Osorno; H. Franz. – FMNH (FMHD #96-248); 4 ♂ and 8 ♀; 15.1 km W Puauchó; 40° 34.97'S 73° 37.68'W; 50 m; 30.XII.1996; A. Newton & M. Thayer 984; valdivian rainforest remnant in sm. ravine, w/large ferns, berlese, leaf & log litter. – FMNH; 4 ♂ and 12 ♀; Puyehue National Park, Antillanca road; 470 m; 20-25.XII.1982; A. Newton & M. Thayer; valdivian rainforest, vouchers associated with larvae, berlese, leaf & log litter, forest floor. – FMNH (FMHD #2002-082); 12 ♂ and 23 ♀; Vicente Perez Rosales National Park, SW slope Volcán Osorno, road to Ref. La Picada; 41° 03.25'S 72° 30.18'W; 660 m; 16.XII.2002; A. Solodovnikov, A. Newton & M. Thayer 1067; *Nothofagus dombeyi* w/conifers dense *Chusquea* bamboo understory, flat area, berlese, leaf & log litter. – MHNG; 17 ♂ and 53 ♀; Puyehue National Park, Anticura Repucura trail; 500 m; 06.II.1985; S. & J. Peck; forest litter. – DBUC; 1 ♀; same data; S. & J. Peck; forest litter. – FMNH (FMHD #85-996, #85-113); 8 ♀; same data; S. & J. Peck. – DBUC; 1 ♂ and 1 ♀; same data; S. & J. Peck. – FMNH; 1 ♂ and 2 ♀; Puyehue National Park, 4.1 km E Anticura, trap site 662; 430 m; 19-26.XII.1982; A. Newton & M. Thayer; valdivian rainforest. – FMNH 1 ♂ and 1 ♀; same data; A. Newton & M. Thayer; valdivian rainforest, window traps. – FMNH; 8 ♂ and 48 ♀; same data; A. Newton & M. Thayer; valdivian rainforest, vouchers associated with larvae, berlese, leaf & log litter, forest floor. – UNHC; 1 ♂; 4.1 km W Anticura, site 663; 270 m; 19-25.XII.1982; A. Newton & M. Thayer; valdivian rainforest, flight intercept (windows) trap. – FMNH; 1 ♂; same data; A. Newton & M. Thayer. – FMNH; 4 ♂ and 4 ♀; same data; A. Newton & M. Thayer; valdivian rainforest, vouchers associated with larvae – FMNH (FMHD #97-40); 17 ♂ and 58 ♀; Puyehue National Park, 4 km E Anticura; 40° 39.73'S 72° 08.10'W; 460 m; 30.I.1997; A. Newton & M. Thayer 985-2; valdivian rainforest w/large, *Saxegothea*, berlese, leaf and log litter. – FMNH (FMHD #97-4); 6 ♂; same data; 01-30.I.1997; A. Newton & M. Thayer 985-2; valdivian rainforest w/large, *Saxegothea*, flight intercept trap. – FMNH (FMHD #97-39); 25 ♂ and 61 ♀; same data; A. Newton & M. Thayer 985-3; valdivian rainforest

w/large, *Saxegothea* berlese, leaf & log litter. – FMNH (FMHD #97-41); 5 ♂ and 9 ♀; same data; 30.I.1997; A. Newton & M. Thayer 985-I; valdivian rainforest w/large, *Saxegothea*, berlese, leaf & log litter. – FMNH (FMHD #96-250); 7 ♂ and 1 ♀; same data; A. Newton & M. Thayer 985-I; valdivian rainforest w/large, *Saxegothea* berlese, flight intercept trap. – FMNH (FMHD #2002-90); 8 ♂ and 14 ♀; Puyehue National Park, Ruta 215; km 4.5 of Aduana station; 40° 40.23'S 72° 05.21'W; 580 m; 19.XII.2002; A. Newton, M. Thayer, D. J. Clarke & M. Chani 1071; valdivian rainforest, berlese, leaf & log litter. – MHNG; 14 ♂ and 76 ♀; Puyehue National Park, Aguas Calientes, Pionero track; 500 m; 28.XII.1984; S. & J. Peck; sifted forest stick litter. – DBUC; 3 ♂; same data; S. & J. Peck. – MHNG; 6 ♂ and 29 ♀; Puyehue National Park, Aguas Calientes, station 25a; 400-500 m; 31.XII.1990/01.I.1991; M. Agosti & D. Burckhardt. – FMNH (FMHD #85-928, #85-43); 4 ♀; Puyehue National Park, Aguas Calientes; 500 m; 20.XII.1984; S. & J. Peck; forest litter on trail, sifting. – PHPC; 5 ♂; Puyehue National Park, 26.2 km E Entre Lagos, near Termas Aguas Calientes; 40° 44.130'S 72° 18.427'W; 460 m; 09-12.III.2008; H. Wood & C. Griswold; sifting litter. – MHNG; 2 ♂ and 3 ♀; Pueatrhue, 65 km W Osorno, station 21; 40° 28'S 73° 43'W; 150 m; 04.XII.1984; D. Burekhardt; valdivian rainforest, sifting of moss on dead tree trunks, branches and rocks and of vegetable detritus. – FMNH (FMHD #85-933, #85-48); 4 ♂ and 11 ♀; 3 km S Maicolpué, Bahía Mansa; 200 m; 21.XII.1984; S. & J. Peck; mixed forest litter, berlese. – MHNG; 20 ♂ and 73 ♀; 3 km S Maicolpué, Bahía Mansa; 21.XII.1984; S. & J. Peck; mixed forest litter. – MHNG; 9 ♂ and 46 ♀; same locality; 03.II.1985; S. & J. Peck. – FMNH; 1 ♂ and 8 ♀; same data, S. & J. Peck. – DBUC; 2 ♂ and 2 ♀; same data; S. & J. Peck. – FMNH (FMHD #96-247); 1 ♂ and 9 ♀; Hills S of Maicolpué; 40° 36.57'S 73° 44.91'W; 160 m; 30.XII.1996; A. Newton & M. Thayer 983; disturbed valdivian rainforest, berlese, leaf & log litter. – UNHC; 2 ♂ and 3 ♀; Hills S of Maicolpué; 160 m; 21.XII.1982; A. Newton & M. Thayer; 2° valdivian forest, berlese, leaf & log litter, forest floor. – FMNH; 3 ♂ and 40 ♀; same data; A. Newton & M. Thayer. – MSNG; 1 ♂ and 2 ♀; Los Ñilques; TC-257; 10.I.1990; T. Cekalovic. – MSNG; 5 ♂ and 11 ♀; same locality; TC-260; 13.I.1990; T. Cekalovic. – MSNG; 1 ♂ and 2 ♀; same locality; TC-553; 17.I.1998; T. Cekalovic. – Región Los Ríos; Ranco prov.: MHNG; 5 ♂ and 21 ♀; 34 km WNW La Unión, station 36; 700 m; 17.XII.1984; S. & J. Peck; litter mixed evergreen forest. – DBUC; 1 ♂ and 2 ♀; same data; S. & J. Peck. – FMNH (FMHD #85-997, #85-114); 1 ♀; 35 km WNW La Unión; 700 m; 07.II.1985; S. & J. Peck; litter mixed evergreen forest, berlese. – Valdivia prov.: UNHC; 2 ♂; Oneol Park; 485 m; 20.I.2001; T. Cekalovic. – PHPC; 8 ♂ and 16 ♀; Oneol Park, 12 km NW Valdivia, Sendero Bonifacio, WDS-T-201; 39° 42'S 73° 19'W; 22.II.2008; W. D. Shepard; sifting litter. – DBUC; 1 ♂ and 1 ♀; same data; W. D. Shepard. – FMNH (FMHD #97-19); 1 ♀; Rincón de La Piedra, turnoff, 14.8 km SE Valdivia; 39° 55' 32''S 73° 06' 27''W; 50 m; 11.I-01.II.1997; A. Newton & M. Thayer 990; disturbed Valdivian rainforest, with *Nothophagus dombeyi* and *Podocarpus saligna*, earthen trap (squid). – FMNH (FMHD #97-20); 3 ♂ and 10 ♀; same locality; 11.I.1997; A. Newton & M. Thayer 990; berlese, leaf & log litter. – FMNH (FMHD #97-42); 1 ♂; same locality; 02.II.1997; A. Newton & M. Thayer 990; disturbed Valdivian rainforest, with *Nothophagus dombeyi* and *Podocarpus saligna*, berlese, litter in ground bromeliad (? *Puya* sp.). leaf axils (live & dead). – Región Araucanía; Cautín prov.: MHNG; 2 ♂; 15 km NE Villarica, Flor del Lago; 500 m; 10.II.1985; S. & J. Peck; forest litter, berlese. – FMNH (FMHD #85-999, #85-116); 1 ♂; same data; S. & J. Peck. – MHNG; 2 ♂ and 3 ♀; 15 km NE Villarica, Flor del Lago, station 16; 300 m; 14.XII.1984; S. & J. Peck; sifted *Boletus* in spruce plantation. – UNHC; 1 ♂ and 1 ♀; Bellavista, North shore Lago Villarica, site 655; 310 m; 15-30.XII.1982; A. Newton & M. Thayer; valdivian rainforest, flood debris forest stream. – FMNH; 2 ♂ and 1 ♀; same data; A. Newton & M. Thayer. – FMNH; 4 ♀; same data; A. Newton & M. Thayer; valdivian rainforest, flood vouchers associated with larvae. – FMNH; 6 ♀; Ñielol National Park, near Temuco, site 652; about 250 m; 14/30.XII.1982; A. Newton & M. Thayer; native forest remnants with *Nothophagus*, vouchers associated with larvae, leaf & log litter, forest floor. – Malleco prov.: MHNG; 4 ♂ and 37 ♀; Purén, Contulmo Natural Monument; 350 m; 13.II.1985; S. & J. Peck; mixed forest litter. – DBUC; 1 ♂ and 2 ♀; same data; S. & J. Peck. – UNHC; 1 ♂; Contulmo National Park, 10 km W Purén; 240 m; 12.

XII.1982; A. Newton & M. Thayer; mixed hdwd. forest with *Chusquea*, berlese, vouchers associated with larvae, leaf & log litter, forest floor. – FMNH; 5 ♂ and 14 ♀; same data; A. Newton & M. Thayer. – FMNH (FMHD #2002-64); 1 ♂ and 5 ♀; Contulmo Natural Monument, Sendero Lemu Mau; 38° 00.74'S 73° 11.13'W; 410 m; 08.XII.2002; A. Newton & A. Solodovnikov 1059; *Nothophagus obliqua-Eucryphia cordifolia* w/fern & bamboo understory, flood debris, small stream. – FMNH; 3 ♀; same data; D. J. Clarke & A. Solodovnikov 1059; *Nothophagus obliqua-Eucryphia cordifolia* w/fern & bamboo understory, sifted litter, hand-collected. – Región Bio Bio; Concepción prov.: MHNG; 12 ♂ and 3 ♀; Pinares; 18.III.1973; T. Cekalovic. – MSNG; 1 ♂ and 2 ♀; El Manzano; TC-329; 08.XI.1992; T. Cekalovic. – Bio Bio prov.: MHNS; 1 ♂ (mislabelled paratypes of *A. globiceps* n° 1659); Pemehue; I.1896; P. Germain. – MNHN; 1 ♀ (sub *A. globocephala*?); Cordillera of Pemehue; 38° 00'S; P. Germain. – Ñuble prov.: MHNS; 1 ♀ (mislabelled paratypes of *A. globiceps* n° 1658); Chillán; P. Germain. – MNHN; 1 ♂ (sub *A. globocephala*?); Cordillera of Chillán, 36° 54'S; P. Germain.

Achilia bifossifrons (Reitter, 1883)

Additional material (1907 ex.): MNHN (coll. Raffray); 3 ♂; Chili. CENTRAL CHILI: Región Aysén: Aysén prov.: MHNG; 1 ♂; 30 km N Puyuhuaipi, station 107; 100 m; 29.I.1985; S. & J. Peck. – Región Los Lagos: Chiloé prov.: MNHN; 1 ♀ (sub *A. lobifera*); Chepu; 42° 03'S; 15.X.1958; G. Kuschel; forest. – MSNG; 2 ♂; Chiloé Island, Chepu; TC-275; 19.II.1991; T. Cekalovic. – MSNG; 3 ♂ and 6 ♀; same locality; TC-580; 09.II.1999; T. Cekalovic. – MSNG; 1 ♂ and 2 ♀; same locality; TC-610; 20.I.2000; T. Cekalovic. – MSNG; 27 ♂ and 13 ♀; same locality; TC-624; 26.I.2000; T. Cekalovic. – MSNG; 29 ♂ and 30 ♀; same locality; TC-625; 26.I.2000; T. Cekalovic. – FMNH (FMHD #97-22); 8 ♂ and 6 ♀; Chiloé Island, SE edge of Tcpuhueico; 42° 48.11'S 73° 55.36'S; 50 m; 15.I.1997; valdivian rainforest; A. Newton & M. Thayer 992; berlese, leaf & log litter. – MSNG; 1 ♀; Mocopulli, SyTC-223; 18.II.1989; S. & T. Cekalovic. – MHNG; 3 ♂ and 1 ♀; Chiloé Island, Huillenco Lake; 31.I.1983; T. Cekalovic. – DBUC; 1 ♂; same data; T. Cekalovic. – MSNG; 3 ♂ and 2 ♀; same locality; TC-278; 21.II.1991; T. Cekalovic. – MSNG; 5 ♂ and 7 ♀; Chiloé Island, 1 km W of Huillenco Lake; TC-564; 24.I.1998; T. Cekalovic. – FMNH (FMHD #2002-72); 1 ♂; S side of Huillenco lake, road to Bellavista; 1.3 km S road of Cucao; 42° 41.81'S 73° 55.88'W; 45 m; 12-22.XII.2002; A. Newton & M. Thayer 1062; valdivian rainforest w/emergent *Saxegothea conspicua*, flight intercept trap. – FMNH (FMHD #2002-74); 1 ♂; same locality; 12.XII.2002; A. Newton & M. Thayer 1062; valdivian rainforest w/emergent *Saxegothea conspicua*, berlese, leaf & log litter. – FMNH (FMHD #2002-092); 4 ♂ and 13 same locality; 22.XII.2002; A. Solodovnikov 1062; valdivian rainforest w/emergent *Saxegothea conspicua*, berlese, leaf & log litter. – FMNH (FMHD #2002-93); same data; A. Solodovnikov 1062; valdivian rainforest w/emergent *Saxegothea conspicua*, berlese, wet debris at stream. – PHPC; 1 ♂; Chiloé Island, Cucao, WDS-T-209; 42° 35'S 74° 05'W; 02.III.2008; W. D. Shepard; litter sifting. – FMNH (FMHD #97-25); 1 ♂; Miraflores, road to (0.6 km W Hwy 5); 42° 46.73'S 73° 47.71'W; 130 m; 17.I.1997; A. Newton & M. Thayer 994; secondary Valdivian rainforest, berlese, leaf & log litter. – FMNH (FMHD #2002-77); 5 ♂ and 3 ♀; same locality; 12.XII.2002; A. Newton & M. Thayer 1063; secondary valdivian rainforest with few conifers, berlese, leaf & log litter. – FMNH (FMHD #97-24); 27 ♂ and 32 ♀; road to Colonia Yungay (3.6 km W Hwy 5); 42° 59'S 73° 41'W; 90 m; 17.I.1997; A. Newton & M. Thayer 995; grazed secondary valdivian rainforest remnants, berlese, leaf & log litter. – FMNH (FMHD #2002-78); 9 ♂ and 23 ♀; road to Colonia Yungay, ca 4 km NW Hwy 5; 42° 59.12'S 73° 42.02'W; 110-115 m; 13.XII.2002; A. Solodovnikov & M. Thayer 1064; disturbed valdivian rainforest w/recent selective cutting, berlese, leaf & log litter. – MSNG; 3 ♂ and 6 ♀; Chiloé Island, Puente La Caldera; TC-466; 15.II.1996; T. Cekalovic. – MSNG; 2 ♂; same locality; TC-524; 18.II.1997; T. Cekalovic. – MSNG; 3 ♂ and 12 ♀; Chiloé Island, 1 km N of Puente Notuco; TC-528; 20.II.1997; T. Cekalovic. – MSNG; 3 ♂ and 11 ♀; Chiloé Island, 5 km SW Chonehi; TC-560; 21.I.1998; T. Cekalovic. – MSNG; 1 ♂ and 2 ♀; same locality; 14.I.1999; T. Cekalovic. – MSNG; 3 ♂ and 11 ♀;

- same locality; TC-623; 25.I.2000; T. Cekalovic. – MSNG; 1 ♂ and 1 ♀; Chiloé Island, Estero Llicaldad; TC-608; 19.I.2000; T. Cekalovic. – MSNG; 3 ♂ and 3 ♀; Chiloé Island, Puente Milildeo; TC-471; 15. II.1995; T. Cekalovic. – MSNG; 5 ♀; Chiloé Island, Estero Tablin; TC-609; 19.I.2000, T. Cekalovic. – MSNG; 4 ♂ and 1 ♀; Quinchao Island, Quetro; TC-582; 12.II.1999, T. Cekalovic. – MSNG; 1 ♂; same locality; TC-559; 20.I.1998; T. Cekalovic. – MSNG; 1 ♂ and 3 ♀; Quinchao Island, Laguna Pulul; C-615; 22.I.2000; T. Cekalovic. – Llanquihue prov.: MNIIN; 1 ♂ and 1 ♀; Los Riscos; 11.IV.1954; G. Kuschel. – FMNH (FMHD #57-125); 1 ♂ and 2 ♀; Río Maullín; III.1957; L. Peña. – MHNS; 2 ♂ (sub mislabelled paratypes of *Achilia globiceps* n° 1650 and 1651); Frutillar; 20.IX.1954; G. Kuschel. – MNHN; 6 ♂; Frutillar; 41° 08'S; 20.IX.1954; G. Kuschel. – MHNG; 11 ♂; Frutillar Bajo, Universidad Chile Forest Reserve; 100 m; 22.XII.1984/02.II.1985; S. & J. Peck; FIT ravine mixed forest. – DBUC; 2 ♂; same data; S. & J. Peck. – FMNH (FMHD #85-935, #85-51); 1 ♂; Frutillar Bajo, Universidad Chile Forest Reserve; 100 m; 22.XII.1984; S. & J. Peck; bracket fungi, berlese. – MHNG; 1 ♂; Petrohué; 30.I.1979; A. De Chambrier. – MIING; 27 ♂ and 62 ♀; Vicente Perez National Park, Salto Petrohué; 150 m; 23.XII.1984; S. & J. Peck; mixed forest litter, berlese. MHNG; 10 ♂ and 21 ♀; same locality; 04.II.1985; S. & J. Peck; mixed forest, sifted litter. – DBUC; 4 ♂; same data; S. & J. Peck. – FMNH (FMHD #85-938, #85-54); 14 ♂ and 17 ♀; same data; S. & J. Peck. – FMNH (FMHD #85-995, #85-112); 5 ♂ and 3 ♀; same data; S. & J. Peck. – UNHC; 1 ♂ and 3 ♀; Saltos Petrohué, 6.4 km SW Petrohué; 140 m; 28.XII.1982; A. Newton & M. Thayer; valdivian rainforest, berlese, leaf & log litter, forest floor. – FMNH (FMHD #97-8); 4 ♂; Vicente Perez Rosales National Park, 9.2 km NE Ensenada, on road to Petrohué; 41° 10.20'S 72° 27.10'W; 125 m; 02-28.I.1997; A. Newton & M. Thayer 987; valdivian rainforest w/ *Nothofagus* spp., flight intercept trap. – FMNH (FMHD #97-10); 7 ♂ and 14 ♀; same locality; 02.I.1997; A. Newton & M. Thayer 987; valdivian rainforest w/ *Nothofagus* spp., berlese, leaf & log litter. – FMNH (FMHD #2002-085); 4 ♂ and 9 ♀; Ensenada, Las Cascadas road, 0.9 km N of La Burbuja; 41° 11.27'S 72° 32.6'W; 80 m; 16.XII.2002; M. Chani; *Nothofagus dombeyi*, mixed hardwoods, berlese, litter. – FMNH (FMHD #97-38); 11 ♂ and 17 ♀; Vicente Perez Rosales National Park, SW slope Vn Osorno, km 4 to La Burbuja; 41° 09.95'S 72° 30.80'W; 310 m; 27.I.1997; A. Newton & M. Thayer 1007; secondary valdivian rainforest w/*Nothofagus dombeyi*- *Eucryphia cordifolia* berlese, leaf & log litter. – MHNG; 1 ♀; La Arena, 45 km SE Puerto Montt; 100 m; 25.XII.1984; S. & J. Peck. – FMNH (FMHD #97-16); 6 ♂ and 26 ♀; Lago Chapo, near SE end, km 9.9 on road from Rollizo; 41° 30.63'S 72° 23.98'W; 385 m; 04.I.1997; A. Newton & M. Thayer 989; valdivian rainforest on steep slope, berlese, leaf & log litter. – MSNG; 1 ♂; Cruce Abtao; SyTC-227; 21.II.1989; S. & T. Cekalovic. – MSNG; 4 ♂ and 5 ♀; Abtao, TC-282; 23.II.1991; T. Cekalovic. – Osorno prov.: FMNH (FMHD #96-248); 4 ♂ and 4 ♀; 15.1 km W Puaicho; 40° 34.97'S 73° 37.68'W; 50 m; 30.XII.1996; A. Newton & M. Thayer 984; valdivian rainforest remnant in sm. ravine, w/large ferns, berlese, leaf & log litter. – MHNG; 1 ♂; Puyehue; 05.XI.1979; A. De Chambrier. – MHNG; 5 ♂ and 3 ♀; Puyehue National Park, Anticura Repucura trail; 500 m; 06. II.1985; S. & J. Peck; forest litter. – DBUC; 2 ♂ and 1 ♀; same data; S. & J. Peck. – FMNH (FMHD #4, #85-113); 8 ♀; same data; S. & J. Peck. – UNHC; 10 ♂ and 2 ♀; Puyehue National Park, 4.1 km E Anticura, trap site 662; 430 m; 19-26.XII.1982; A. Newton & M. Thayer; valdivian rainforest, screen sweeping. – FMNH; 3 ♂; same data; A. Newton & M. Thayer; valdivian rainforest, screen sweeping at dusk. – FMNH; 30 ♂ and 85 ♀; same data; A. Newton & M. Thayer; valdivian rainforest, voucher associated with larvae, berlese, leaf and log litter. – A. Newton & M. Thayer; valdivian rainforest, FMNH; 8 ♂; same data; A. Newton & M. Thayer; valdivian rainforest, window trap 662. – FMNH (FMHD# 96-250); 166 ♂; Puyehue National Park, 4 km E Anticura; 40° 39.73'S 72° 08.10'W; 460 m; 30.XII.1996/30.I.1997; A. Newton & M. Thayer 985-1; valdivian rainforest w/large, *Saxegothea*, flight intercept trap. – FMNH (FMHD #97-5); 101 ♂; same locality; 30.I.1997; A. Newton & M. Thayer 985-3; valdivian rainforest w/large, *Saxegothea*, flight intercept trap. – FMNH (FMHD# 97-4); 14 ♂ and 1 ♀; same data; A. Newton & M. Thayer 985-2; valdivian rainforest w/ large, *Saxegothea*, flight intercept trap. – FMNH (FMHD# 97-39); 65 ♂ and 108 ♀; same locality; 30.I.1997; A. Newton & M. Thayer 985-3; valdivian rainforest w/large, *Saxegothea* berlese, leaf & log litter. – FMNH (FMHD# 97-40); 21 ♂ and 65 ♀; same locality; 30.I.1997; A. Newton & M. Thayer 985-2; valdivian rainforest w/large, *Saxegothea*, berlese, leaf and log litter – FMNH (FMHD# 97-41); 25 ♂ and 18 ♀; same data; A. Newton & M. Thayer 985-1; valdivian rainforest w/large, *Saxegothea*, berlese, leaf & log litter. – MHNG; 15 ♂ and 9 ♀; Puyehue National Park, Aguas Calientes, Pionero track; 500 m; 28.XII.1984; S. & J. Peck; sifted forest stick litter. – FMNH (FMHD # 85-928, #85-43); 1 ♂ and 1 ♀; same data; S. & J. Peck. – FMNH (FMHD #2002-090); 11 ♂ and 24 ♀; Puyehue National Park, Ruta 215; km 4.5 of Aduana station; 40° 40.23'S 72° 05.21'W; 580 m; 19.XII.2002; A. Newton, M. Thayer, D. J. Clarke & M. Chani 1071; valdivian rainforest, berlese, leaf & log litter. – FMNH; 2 ♂ and 3 ♀; Puyehue National Park, Antillanca road; 470 m; 20-25.XII.1982; A. Newton & M. Thayer; valdivian rainforest, berlese, vouchers associated with larvae, leaf & log litter, forest floor. – MHNG; 3 ♂; Puyehue National Park, Antillanca road; 500-1000 m; 18-20.XII.1984; S. & J. Peck; car netting. – FMNH (FMHD #85-923, #85-38); 1 ♂; same data; S. & J. Peck. – MHNG; 6 ♂ and 25 ♀; Puyehue National Park, Aguas Calientes, station 25a; 400-500 m; 31.XII.1990/01.I.1991; M. Agosti & D. Burckhardt. – PHPC; 3 ♂ and 5 ♀; Puyehue National Park, near Termes Aguas Calientes, 26.2 km E Entre Lagos; 40° 44.130'S 72° 18.427'W; 460 m; 09-12. III.2008; H. Wood & C. Griswold. – UNHC; 1 ♂; 7.7 km NE Termas de Puyehue, site 664; 200 m; 19-25.XII.1982; A. Newton & M. Thayer; valdivian rainforest, berlese, leaf & log litter, forest floor. – MHNG; 1 ♂; Umg. Osorno; H. Franz. – MHNG; 3 ♂ and 13 ♀; Pucatrihue, 65 km W Osorno, station 21; 40° 28'S 73° 43'W; 150 m; 04.XII.1984; D. Burckhardt; valdivian rainforest, sifting of moss on dead tree trunks, branches and rocks and of vegetable detritus. – MHNG; 32 ♂ and 123 ♀; 3 km S Maicolpué, Bahía Mansa; 200 m; 03.II.1985; S. & J. Peck; mixed forest litter. – FMNH (FMHD #85-994, #85-111); 1 ♂ and 1 ♀; same data; S. & J. Peck. – FMNH (FMHD # 96-247); 1 ♂ and 1 ♀; Hills S of Maicolpué; 40° 36.57'S 73° 44.91'W; 160 m; 30.XII.1996; A. Newton & M. Thayer 983; disturbed valdivian rainforest, berlese, leaf & log litter. – MSNG; 1 ♂ and 1 ♀; Los Ñilques; TC-553; 17.I.1998, T. Cekalovic. – Región Los Ríos: Ranco prov.: FMNH (FMHD #85-921, #85-36); 1 ♀; 34 km WNW La Unión; 700 m; 17.XII.1984; S. & J. Peck; litter mixed forest, berlese. – UNHC; 3 ♂ and 1 ♀; 4.1 km W Anticura, site 663; 270 m; 19-25.XII.1982; A. Newton & M. Thayer; valdivian rainforest, flight intercept (windows) trap. – FMNH; 1 ♂ and 16 ♀; same data; A. Newton & M. Thayer; valdivian rainforest, voucher associated with larvae. – Valdivia prov: MHNG; 1 ♂; 35 km N Valdivia; 12.V.1979; T. Cekalovic. – DBUC; 1 ♂ and 2 ♀; same data; T. Cekalovic. – FMNH (FMHD #97-42); 1 ♂; Rincón de La Piedra, turnoff, 14.8 km SE Valdivia; 39° 55' 32"S 73° 06' 27"W; 50 m; 02. II.1997; A. Newton & M. Thayer 990; disturbed Valdivian rainforest, with *Nothofagus dombeyi* and *Podocarpus saligna*, berlese, litter in ground bromeliad (? *Puya* sp.). leaf axils (live & dead). – FMNH (FMHD #97-18); 1 ♂; same data; 11.I-01.II.1997; A. Newton & M. Thayer 990; disturbed Valdivian rainforest, with *Nothofagus dombeyi* and *Podocarpus saligna*, flight intercept (windows) trap. – FMNH; 1 ♂; Casa de Piedra, Lago Calafquen; 26.I.1995; T. Cekalovic. – Región Araucanía: Cautín prov.: MHNG; 4 ♂; 15 km NE Villarica, Flor del Lago; 300 m; 14.XII.1984/10.II.1985; S. & J. Peck; 2 FIT *Nothofagus* forest. – FMNH (FMHD #85-999, #85-116); same data; 1 ♂ and 1 ♀; S. & J. Peck. – MHNG; 2 ♂; same locality; 14.XII.1984; S. & J. Peck; sifting litter *Nothofagus* forest. – MHNG; 1 ♂ and 2 ♀; 15 km NE Villarica, Flor del Lago, station 16; 500 m; 10.II.1985; S. & J. Peck; sifting forest litter. – UNHC; 2 ♂ and 1 ♀; Bellavista, North shore Villarica Lake, site 655; 310 m; 15-30.XII.1982; A. Newton & M. Thayer; valdivian rainforest, flood debris forest stream. – FMNH; 4 ♂ and 3 ♀; same data; A. Newton & M. Thayer; valdivian rainforest, vouchers associated with larvae. – MHNG; 5 ♀; Huerquehue National Park, station 17a; 800 m; 22-25.XII.1980; M. Agosti & D. Burckhardt; forest litter. – DBUC; 2 ♂; same data; M. Agosti & D. Burckhardt. – FMNH; 1 ♂ and 4 ♀; Ñielol National Park, near Temuco, site 652; about 250 m; 14/30.XII.1982; A. Newton & M. Thayer; native forest remnants with *Nothofagus*, vouchers associated with larvae, leaf & log litter, forest floor. – FMNH (FMHD #85-909, P#85-23); 1 ♀; Cerro Ñielol National Park, Temuco; 300 m; 13.XII.1984; S. & J. Peck; mixed forest litter. – Malleco prov.: MHNG; 6 ♂; 17 km W Angol;

800 m; 08.XII.1984/16.II.1985; S. & J. Peck; FIT mixed *Nothophagus*. – DBUC; 1 ♂; same data; S. & J. Peck. – MHNG; 1 ♂; Nahuelbuta National Park, 45 km W Angol; 1400 m; 09.XII.1984/16.II.1985; S. & J. Peck; *Nothophagus-Araucaria* forest, car trap. – MHNG; 1 ♀; Purén, Contulmo Natural Monument; 350 m; 13.II.1985; S. & J. Peck; mixed forest litter. – MHNG; 3 ♂; Purén, Contulmo Natural Monument; 300-600 m; 11.XII.1984/13.II.1985; S. & J. Peck; FIT mixed evergreen forest & MT *Nothophagus* forest. – FMNH (FMHD# 2002-64); 1 ♂ and 3 ♀; Contulmo Natural Monument, Sendero Lemu Mau; 38° 00.74'S 73° 11.13'W; 410 m; 08.XII.2002; A. Newton & A. Solodovnikov 1059; *Nothophagus obliqua-Eucryphia cordifolia* w/fern & bamboo understory, flood debris, small stream – Región Bío Bío: Arauco prov.: MSNG; 14 ♂ and 24 ♀; Río Caramávida; TC-588; 21.III.1999; T. Cekalovic. – Concepción prov.: MHNG; 10 ♂ and 16 ♀; Pinares; 18.III.1973; T. Cekalovic. – DBUC; 1 ♂ and 1 ♀; same data; T. Cekalovic. – MHNG; 1 ♂; Pinares; 20.XII.1970; T. Cekalovic. – MHNG; 1 ♂ and 1 ♀; Hualpén; 05.III.1973; T. Cekalovic. – FMNH; 2 ♂ and 2 ♀; Puente Pelun, TC-342; 18.I.1993; T. Cekalovic. – MSNG; 7 ♂ and 4 ♀; Puente Pelun; TC-358; 21.II.1993; T. Cekalovic. – MSNG; 1 ♂ and 3 ♀; Chiguayante; TC-236; 11.IX.1990; T. Cekalovic. – MSNG; 1 ♂; Estero Nonguén; TC-460; 27.I.1996; T. Cekalovic. – MSNG; 10 ♂ and 5 ♀; same locality; TC-462; 06.II.1996; T. Cekalovic. – MSNG; 1 ♂ and 1 ♀; same locality; TC-540; 26.III.1997; T. Cekalovic. – MSNG; 7 ♂ and 3 ♀; same locality; TC-541a; 27.III.1997; T. Cekalovic. – MSNG; 1 ♂; Concepción, Lonco; TC-245; 01.XI.1989; T. Cekalovic. – MSNG; 1 ♀; Periquillo; TC-311; 15.IX.1992; T. Cekalovic. – Ñuble prov.: MNHN; 1 ♀ (sub *A. frontalis*); Cordillera of Chillán; 36° 54'S; P. Germain.

Achilia lobifera Jeannel, 1962

Additional material (371 ex.): SOUTHERN CHILE: Región Magallanes y de la Antártica Chilena: Última Esperanza prov.: MHNS; 2 ♀ (mislabelled paratypes of *Achilia lobifera* n° 1667 and 1668) – MHNS; 1 ♀ (mislabelled paratype of *Achilia lobifera* n° 1660); Carlos Islet; 08.XII.1958; G. Kuschel. – CENTRAL CHILE: Región Aysén: General Carrera prov.: MNHN; 1 ♂ and 1 ♀; Río Murta, NW end of Buenos Aires Lake; 46° 28'S; 25.I.1956; G. Kuschel; forest. – Aysén prov.: MHNG; 9 ♂ and 7 ♀; 30 km N Puyuhuapi, station 107; 100 m; 29.I.1985; S. & J. Peck; sifted moss on logs. – FMNH (FMHD #85-990, #85-107); 2 ♂; same data; S. & J. Peck. – DBUC; 1 ♂; same data; S. & J. Peck. – MHNG; 1 ♂; 16 km NW Cisnes Medio, Río Grande; 200 m; 30.XII.1984-28.I.1985; S. & J. Peck; FIT mature beech forest. – Región Los Lagos: Palena prov.: FMNH (FMHD #97-31); 1 ♀; Austral Highway km 60.2 (4.0 km S Contao turnoff); 41°49.87'S 72°42.33'W; 140 m; 23.I.1997; A. Newton & M. Thayer 1001; young secondary valdivian rainforest, berlese, leaf & log litter. – FMNH (FMHD #97-32); 1 ♂ and 4 ♀; Austral Highway km 67.9 (11.7 km S Contao turnoff); 41°55'S 72°42'W; 220 m; 23.I.1997; A. Newton & M. Thayer 1002; young secondary valdivian rainforest, berlese, leaf & log litter. – FMNH (FMHD #97-33); 3 ♂ and 6 ♀; Austral Highway km 84.0 (17.8 km W Hornopirén); 42°00.57'S 72°37.02'W; 140 m; 23.I.1997; A. Newton & M. Thayer 1003; disturbed valdivian rainforest near ridge-top, berlese, leaf & log litter. – Chiloé prov.: MHNG; 1 ♂; Chiloé; H. Franz. – MHNG; 1 ♂ and 2 ♀; Chiloé National Park, Cucao, 30 km SW Castro, station 29a; 30 m; 04-06.I.1991; M. Agosti & D. Burckhardt; temperate rainforest. – MHNG; 1 ♀; Chiloé National Park, 30 km SW Castro, near Cucao, station 34b; 42° 37'S 74° 08'W; 10-70 m; 28.XII.1992/01.I.1993; D. Burckhardt; sifting of moss on forest floor trees and dead trunks and vegetational debris. – FMNH (FMHD #97-23); 2 ♂ and 1 ♀; Quemchi, 11 km W of (11 km E Hwy 5); 42° 10.42'S 73° 35.81'W; 170 m; 16.I.1997; A. Newton & M. Thayer 993; secondary valdivian rainforest, berlese, leaf & log litter. – FMNH (FMHD #2002-068); 2 ♂ and 12 ♀; Quemchi, 11 km W of (11 km E Hwy 5); 42° 10.40'S 73° 35.73'W; 140 m; 10.XII.2002; A. Solodovnikov & A. Newton 1060; valdivian rainforest remnant w/thick bamboo understory; berlese, leaf & log litter. – Llanquihue prov.: MHNG; 2 ♂ and 6 ♀; Alerce Andino National Park, above Laguna Chaiquenes, station 37; 41° 40'S 72° 35'W; 350-650 m; 04.I.1993; D. Burckhardt; mixed *Fitzroya cupressoides* forest with thick moss cover inside, sifting of moss on floor and tree trunks and vegetational debris. – MHNG; 1 ♀;

Alerce Andino National Park, road from park entrance to Laguna Chaiquenes, station 36b; 41° 40'S 72° 35'W; 200-350 m; 03-06.I.1993; D. Burckhardt; sifting of moss on rock, dead wood and forest floor and of vegetational debris. – MHNG; 3 ♂ and 3 ♀; Alerce Andino National Park, Laguna Triángulo, station 38b; 41° 40'S 72° 35'W; 550 m; 05-06.I.1993; D. Burckhardt; sclerophyll rainforest, sifting of moss on tree trunks and of vegetational debris. – FMNH (FMHD #97-30); 1 ♂; Alerce Andino National Park, N side Laguna Sargazo; 41° 30'S 72° 36'W; 400 m; 21.I.1997; A. Newton & M. Thayer 1000; *Fitzroya cupressoides* w/valdivian rainforest understory steep slope, berlese, leaf & log litter. – UNHC; 1 ♂; Lago Chapo, 13.5 km E Correntoso, site 656; 310 m; 16-27.XII.1982; A. Newton & M. Thayer; valdivian rainforest, flight intercept (windows) trap. – FMNH (FMHD #97-16); 1 ♂ and 5 ♀; Lago Chapo, near SE end, km 9.9 on road from Rollizo; 41° 30.63'S 72° 23.98'W; 385 m; 04.I.1997; A. Newton & M. Thayer 989; valdivian rainforest on steep slope, berlese, leaf & log litter. – FMNH (FMHD #97-26); 16 ♂ and 9 ♀; Lago Chapo, 1.2 km N of NW end; 41° 25'S 72° 35'W; 265 m; 19.I.1997; A. Newton & M. Thayer 996; small secondary *Nothofagus dombeyi* w/valdivian rainforest understory, berlese, leaf & log litter. – FMNH (FMHD #97-39); 1 ♀; Puerto Montt, 50 km SW on Hwy 5, 0.7 km NE jct. to Maullín; 41° 43.20'S 73° 22.27'W; 60 m; 20.I.1997; A. Newton & M. Thayer 999; secondary valdivian rainforest remnants, berlese, leaf & log litter. – Osorno prov.: MHNG; 8 ♂ and 7 ♀; Puyehue National Park, Aguas Calientes, station 20b; 40° 40'S 72° 20'W; 450-600 m; 01-03.XII.1992; D. Burckhardt; moss on dead tree trunks, branches and rocks and of vegetable detritus. – MHNG; 17 ♂ and 17 ♀; Puyehue National Park, road Aguas Calientes-Antillanca, station 19b; 40° 45'S 72° 15-20'W; 750-850 m; 30.XI/01.XII.1992; D. Burckhardt; sifting of moss on tree trunks and forest floor and vegetational debris. – MHNG; 13 ♂ and 16 ♀; Puyehue National Park, Aguas Calientes to Antillanca, station 28a; 800 m; 02.I.1991; M. Agosti & D. Burckhardt. – DBUC; 1 ♂ and 2 ♀; same data; M. Agosti & D. Burckhardt. – MHNG; 2 ♂; Puyehue National Park, Aguas Calientes, Los Derrumbes forest; 500 m; 20.XII.1984/08.II.1985; S. & J. Peck; FIT. – FMNH (FMHD #96-246); 1 ♂; Puyehue National Park, Antillanca road, 7.2 km above Aguas Calientes, 40° 45.55'S 72° 17.82'W; 660 m; 29.XII.1996; A. Newton & M. Thayer 982; valdivian rainforest w/ *Saxegothea* dominant, dense *Chusquea*, berlese, leaf & log litter. – MHNG; 5 ♂; Puyehue National Park, Antillanca road; 500-1000 m; 18-20.XII.1984; S. & J. Peck; car netting. – MHNG; 3 ♂; Puyehue National Park, Antillanca road; 600-1000 m; 20.XII.1984; S. & J. Peck; car netting. – UNHC; 1 ♂; Puyehue National Park, Antillanca road, site 659; 720 m; 18-24.XII.1982; A. Newton & M. Thayer; *Nothofagus* spp. forest, flight intercept (windows) trap. – FMNH; 2 ♂ and 7 ♀; Puyehue National Park, Antillanca road, site 660; 845 m; 18-24.XII.1982; *Nothofagus Saxegothea* forest, berlese; A. Newton & M. Thayer; leaf & log litter, forest floor. – UNHC; 1 ♂; Puyehue National Park, Antillanca road, site 661; 690 m; 18-24.XII.1982; A. Newton & M. Thayer; valdivian rainforest, window trap. – FMNH (FMHD #97-1); 4 ♂ and 5 ♀; Puyehue National Park, Antillanca road, approaching ski center; 40° 46.85'S 72° 13.03'W; 980 m; 01.I-01.II.1997; A. Newton & M. Thayer 986; open *Nothofagus pumilio* forest w/*Chusquea*, flight intercept trap. – FMNH (FMHD #97-3); 1 ♂ and 22 ♀; same locality; 01.I.1997; A. Newton & M. Thayer 986; open *Nothofagus pumilio* forest w/dense *Chusquea*, berlese, leaf & log litter. – FMNH (FMHD #2002-82); 12 ♂ and 8 ♀; Vicente Perez Rosales National Park, SW slope Volcán Osorno, road to Ref. La Picada; 41° 03.25'S 72° 30.18'W; 660 m; 16.XII.2002; A. Solodovnikov, A. Newton & M. Thayer 1067; *Nothofagus dombeyi* w/conifers dense *Chusquea* bamboo understory, flat area, berlese, leaf & log litter. – DBUC; 4 ♂ and 4 ♀; same data; A. Solodovnikov, A. Newton & M. Thayer 1067. – FMNH; 3 ♂ and 1 ♀; Vicente Perez Rosales National Park, SW slope Volcán Osorno, road to Ref. La Picada; 41° 01.05'S 72° 32.90'W; 430 m; 16.XII.2002; M. Thayer, A. Newton & D. J. Clarke 1068; *Nothofagus dombeyi* w/conifers, pyr.-fogging old logs & stump. – FMNH (FMHD #2002-083); 6 ♂ and 20 ♀; same data; A. Newton, A. Solodovnikov & M. Chani 1068; *Nothofagus dombeyi* w/conifers, berlese, leaf & log litter. – FMNH (FMHD #97-12); 1 ♂; Vicente Perez Rosales National Park, SW slope Vn Osorno, km 10.1 to La Burbuja; 41° 08.30'S 72° 32.15'W; 925 m; 03-27.I.1997; A. Newton & M. Thayer 988; *Nothofagus dombeyi* & *Podocarpus nubigena* w/valdivian

rainforest understory, carrion trap (squid). – FMNH (FMHD #2002-81); 1 ♂ and 2 ♀; Vicente Perez Rosales National Park, SW slope Volcán Osorno, km 10 to La Burbuja; 41° 08.33'S 72° 32.16'W; 910 m; 15.XII.2002; M. Thayer & A. Solodovnikov 1066; *Nothofagus dombeyi* w/mixed understory, berlese, leaf & log litter. – FMNH (FMHD #97-35); 1 ♂ and 3 ♀; Vicente Perez Rosales National Park, SW slope Vn Osorno, km 11 to La Burbuja; 41° 07.91'S 72° 32.16'W; 1065 m; 27.I.1997; A. Newton & M. Thayer 1005; low *Nothofagus dombeyi* w/ mixed understory, berlese, leaf & log litter. – FMNH (FMHD #97-4); 1 ♂; Puyehue National Park, 4 km E Anticura; 40° 39.73'S 72° 08.10'W; 460 m; Newton & M. Thayer 985-2; valdivian rainforest w/large, *Saxegothea*, flight intercept trap. – FMNH (FMHD #97-40); 2 ♂; same locality; 30.I.1997; A. Newton & M. Thayer 985-2; valdivian rainforest w/large, *Saxegothea*, berlese, leaf and log litter. – FMNH (FMHD #97-39); 2 ♂; same locality; 30.I.1997; A. Newton & M. Thayer 985-3; valdivian rainforest w/large, *Saxegothea* berlese, leaf & log litter. – FMNH (FMHD #97-5); 1 ♂; same locality; 30.I.1997; A. Newton & M. Thayer 985-3; valdivian rainforest w/large, *Saxegothea*, flight intercept trap. – FMNH (FMHD #2002-88); 9 ♂; Puyehue National Park, Ruta 215; near Laguna Las Mellizas; 40° 40.8'S 71° 59.4'W; 1000 m; 19. XII.2002; A. Newton & M. Thayer 1070; *Nothofagus pumilio* forest w/ dense bamboo understory, berlese, wet debris in large stream. – DBUC; 2 ♂; same data; A. Newton & M. Thayer 1070. – FMNH (FMHD #2002-90); 17 ♂ and 11 ♀; Puyehue National Park, Ruta 215; km 4.5 of Aduana station; 40° 40.23'S 72° 05.21'W; 580 m; 19.XII.2002; A. Newton, M. Thayer, D. J. Clarke & M. Chani 1071; valdivian rainforest, berlese, leaf & log litter. – MHNG; 1 ♀; Puyehue National Park, sector Mirador Los Mallines, station 72a; 700 m; 01-03.II.1996; D. Burckhardt; open *Nothofagus nitida* scrub intergrading into sclerophyll rainforest sifting of moss and vegetational debris. – Región Araucanía: Cautín prov.: MHNG; 1 ♂ and 4 ♀; Huerquehue National Park, station 16a; 800-900 m; 22-24.XII.1980; M. Agosti & D. Burckhardt; forest litter. – DBUC; 1 ♀; same data; M. Agosti & D. Burckhardt. – FMNH (FMHD #96-239); 2 ♂ and 4 ♀; Villarica National Park, Volcán Villarica, road to sky center; 39° 22.48'S 71° 58.30'W; 1180 m; 26.XII.1996; A. Newton & M. Thayer 980; *Nothofagus dombeyi* forest w/*Chusquea*, berlese, leaf & log litter. – FMNH (FMHD #96-237); 1 ♂; same locality; 26.XII.1996/03.II.1997; A. Newton & M. Thayer 980; *Nothofagus dombeyi* forest w/*Chusquea*, flight intercept trap.

Achilia antennalis Jeannel, 1962

Additional material (124 ex.): CENTRAL ARGENTINA: Neuquén prov.: MNHN; 1 ♂; Saint Martin de los Andes, Lanin reserve; about 40° S; 1000 m; III.1959; specimens wandering on the sandy shores of Lacar Lake; C. Delamare. – MHNS; 1 ♂ (mislabelled as paratype of *A. antennalis* n° 1679); Saint Martin de los Andes, Lanin reserve; III.1959; C. Delamare. – MNHN; 1 ♂; Chile. MNHN; 1 ♂; Chile; P. Germain. CENTRAL CHILE: Región Los Lagos: Osorno prov.: MHNG; 1 ♂ and 1 ♀; Puyehue National Park, Anticura Repucura trail; 500 m; 06.II.1985; S. & J. Peck; forest litter. – FMNH (FMHD #2002-087); 5 ♂; Puyehue National Park, W side Paso Cardenal Samoré; 40° 42.65'S 71° 56.66'W; 1305 m; 17.XII.2002; A. Newton, M. Thayer & A. Solodovnikov 1069; timberline *Nothofagus pumilio* forest with snow patches, berlese, leaf & log litter. – FMNH (FMHD #2002-88); 5 ♂; Puyehue National Park, Ruta 215; near Laguna Las Mellizas; 40° 40.8'S 71° 59.4'W; 1000 m; 19.XII.2002; A. Newton & M. Thayer 1070; *Nothofagus pumilio* forest w/ dense bamboo understory, berlese, wet debris in large stream. – FMNH (FMHD #96-244); 1 ♂; Puyehue National Park, Antillanca road, 7.2 km above Aguas Calientes, 40° 45.55'S 72° 17.82'W; 660 m; 29.XII.1996/01.II.1997; A. Newton & M. Thayer 982; valdivian rainforest w/ *Saxegothea* dominant, dense *Chusquea*, flight intercept trap. – FMNH (FMHD #96-246); 1 ♂; same locality; 29.XII.1996; A. Newton & M. Thayer 982; valdivian rainforest w/ *Saxegothea* dominant, dense *Chusquea*, berlese, leaf & log litter. – FMNH (FMHD #97-41); 2 ♂; Puyehue National Park, 4 km E Anticura; 40° 39.73'S 72° 08.10'W; 460 m; 30.I.1997; A. Newton & M. Thayer 985-1; valdivian rainforest w/large, *Saxegothea*, berlese, leaf & log litter. – Región Araucanía: Cautín prov.: MHNG; 1 ♂; Conguillío National Park, station 12a; 950 m; 19-21.XII.1990; M. Agosti & D.

Burckhardt; forest litter. – MHNG; 1 ♂; Conguillío National Park, Playa Linda, station 13b; 1150 m; 19-20.XII.1990; M. Agosti & D. Burckhardt; *Nothofagus* ant. forest. – FMNH (FMHD #96-228); 2 ♂ and 15 ♀; Conguillío National Park, 11.1 km SE Laguna Captrén guard sta.; 38° 40.05'S 71° 37.21'W; 1080 m; 23.XII.1996; A. Newton & M. Thayer 976; *Nothofagus obliqua* & *alpina*, dense *Chusquea* understory, berlese, leaf & log litter. – DBUC; 2 ♀; same data; A. Newton & M. Thayer 976. – FMNH (FMHD #96-232); 1 ♂; Conguillío National Park, 4.0 km E Laguna Captrén guard sta.; 38° 38.98'S 71° 39.77'W; 1255 m; 23.XII.1996/05.II.1997; A. Newton & M. Thayer 976; *Nothofagus dombeyi* forest, berlese, flood debris along stream. – MHNG; 1 ♂; Huerquehue National Park, station 16a; 800-900 m; 22-24. XII.1990; M. Agosti & D. Burckhardt; forest litter. – MHNG; 1 ♂ and 1 ♀; Huerquehue National Park, Lago Cicho, station 18a; 1250-1350 m; 23.XII.1990; M. Agosti & D. Burckhardt; forest litter. – MHNG; 1 ♂; 15 km NE Villarrica, Flor del Lago; 300 m; 14.XII.1984/10.II.1985; S. & J. Peck; *Nothofagus* forest. – FMNH (FMHD #96-237); 8 ♂; Villarica National Park, Volcán Villarica, road to sky center; 39° 22.48'S 71° 58.30'W; 1180 m; 26.XII.1996/03.II.1997; A. Newton & M. Thayer 980; *Nothofagus dombeyi* forest w/*Chusquea*, flight intercept trap. – FMNH (FMHD #96-241); 4 ♂; Villarica National Park, Volcán Villarica, road to sky center; 39° 23.27'S 71° 57.82'W; 1390 m; 27.XII.1996/03.II.1997; A. Newton & M. Thayer 981; *Nothofagus pumilio* forest, flight intercept trap. – FMNH (FMHD #96-243); 1 ♂ and 1 ♀; same locality; 27.XII.1996; A. Newton & M. Thayer 981; stunted *Nothofagus pumilio* forest, berlese, leaf & log litter. – UNHC; 2 ♂ and 4 ♀; Volcán Villarica, site 653; 1250 m; 15-29.XII.1982; A. Newton & M. Thayer; *Nothofagus dombeyi* and *pumilio* forest with *Chusquea*, berlese, leaf & log litter, forest floor. – FMNH; 2 ♂ and 3 ♀; same data; A. Newton & M. Thayer. – DBUC; 1 ♂ ad 1 ♀; same data; A. Newton & M. Thayer. – UNHC; 2 ♂; Volcán Villarica, site 654; 1120 m; 15-29.XII.1982; A. Newton & M. Thayer; *Nothofagus dombeyi* and *Saxegothea* forest with *Drimys*, flight intercept (windows) trap. – FMNH; 2 ♂; same data; A. Newton & M. Thayer. – Malleco prov.: MHNG; 1 ♂; Princesa, 20 km W CuraCautín; 1000 m; 12.XII.1984/16. II.1985; S. & J. Peck; *Nothofagus* forest. – FMNH (FMHD #97-46); 8 ♂ and 14 ♀; Conguillío National Park, 4.9 km of N entrance (road from CuraCautín); 38° 37.84'S 71° 43.31'W; 1210 m; 05.II.1997; A. Newton & M. Thayer 1009; *Araucaria-Nothofagus* forest on ash/lava; berlese, litter under *Araucaria araucana*. – FMNH (FMHD #85-905, #85-19); 4 ♂; 40 km W CuraCautín; 1500 m; 12.XII.1984/16.II.1985; S. & J. Peck; *Nothofagus-Araucaria*, malaise. – DBUC; 1 ♂; same data; S. & J. Peck. – MHNG; 1 ♂; environs of Malalcahuello; H. Franz. – UNHC; 1 ♂; 6.5 km E Malalcahuello, site 651; 1080 m; 13-31.XII.1982; A. Newton & M. Thayer; *Nothofagus dombeyi* forest with *Chusquea*, berlese, leaf & log litter, forest floor. – FMNH; 1 ♂; same data; S. & J. Peck. – FMNH (FMHD #96-236); 1 ♂; Malalcahuello, 11.1 km E of on road to Lonquimay; 38° 26.32'S 71° 30.11'W; 1350 m; 24.XII.1996; A. Newton & M. Thayer 979; *Nothofagus dombesyi-Araucaria araucana* forest selectively logged, leaf & log litter. – FMNH; 1 ♂; Tolhuaca National Park, Lago Malleco; 890-925 m; 01.I.1983; A. Newton & M. Thayer; *Nothofagus* forest, berlese, leaf & log litter, forest floor. – MHNG; 1 ♂; Purén, Contulmo Natural Monument; 300-600 m; 11.XII.1984/13.II.1985; S. & J. Peck; FIT mixed evergreen forest & MT *Nothofagus* forest. – MNSG; 2 ♂; Salto del Indio; TC-230; 10.III.1989; T. Cekalovic. – Región Bío Bío: Bío Bío prov.: MNHN; 1 ♂; Pemehue; 38° 00'S; P. Germain. – Ñuble prov.: MHNS; 1 ♂ (mislabelled as paratype of *A. antennalis* n° 1684); Chillán; P. Germain. – Región Maule: Talca prov.: FMNH (FMHD #96-208); 1 ♂; Area de Protección Vilches, Piedras Tacitas area; 35° 36.53'S 71° 04.10'W; 1185 m; 17.XII.1996; A. Newton & M. Thayer 101 *Nothofagus* spp. with shrubs along stream, berlese, leaf & log litter. – FMNH (FMHD #96-209); 3 ♂ and 7 ♀; same locality; 17.XII.1996; A. Newton & M. Thayer 1011; *Nothofagus* spp. with shrubs along stream, berlese, wet litter at seep. – DBUC; 1 ♂ and 2 ♀; same data; A. Newton & M. Thayer 1011.

New genera and new species of the family Linyphiidae from Borneo, Sumatra and Java
(Arachnida, Araneae)

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Abstract: Two new genera and seven new species of the family Linyphiidae from the collections of the Muséum d’histoire naturelle de Genève are described: *Kalinagone* gen. nov. with *Kalinagone cuspidata* sp. nov. (the type species) and *K. rotunda* sp. nov. from Borneo; *Tegulinus* gen. nov. with *Tegulinus sumatranus* sp. nov. (the type species) and *T. bifurcatus* sp. nov. from Sumatra; *Dumoga buratino* sp. nov. and *Prosoponoides jaubi* sp. nov. from Sumatra; and *Oedothorax bifoveatus* sp. nov. from Borneo and Java. A list of the linyphiid species currently known from Borneo, Sumatra and Java is presented.

Keywords: Erigoninae - Linyphiinae - Southeast Asia - East Malaysia - Indonesia.

INTRODUCTION

At present, about 140 linyphiid species from 69 genera have been described or recorded from Southeast Asia (see Locket, 1982; Millidge & Russell-Smith, 1992; Barrion & Litsinger, 1995; Millidge, 1995; Helsdingen, 1969, 1985a, b; Heimer, 1984; Saaristo & Tanasevitch, 2003a, b; Tu & Li, 2004; Tanasevitch, 2014a, b, 2015, 2016, 2017). The present paper adds to this list another two new genera and seven new species, which are here described from Borneo, Sumatra and Java. According to new data the linyphiid faunas of these islands are currently known to contain 24, 26 and 12 species, respectively (see Table 1).

MATERIAL AND METHODS

This paper is based on material kept at the Muséum d’histoire naturelle de Genève, Switzerland (MNHG). Specimens preserved in 70% ethanol were studied using a MBS-9 stereomicroscope. A Levenhuk C-800 digital camera was used for some drawings. Images taken at multiple focal planes were combined using the Helicon Focus image stacking software, version 5.1. Sample numbers are given in square brackets. The terminology of copulatory organs mainly follows that of Merrett (1963), Hormiga (1994, 2000) and Tanasevitch (2015). The chaetotaxy is given in a formula, e.g.,

2.2.1.1, which refers to the number of dorsal spines on tibiae I-IV. The sequence of leg segment measurements is as follows: femur + patella + tibia + metatarsus + tarsus. All measurements are given in mm. Figure numbers are given above the scale lines, the corresponding distance below.

Abbreviations

- a.s.l. Above sea level
- C Convector *sensu* Tanasevitch (1998) = lamella *sensu* Merrett (1963)
- DAC Distal apophysis of convector *sensu* Tanasevitch (2015)
- DSA Distal suprategular apophysis *sensu* Hormiga (2000)
- E Embolus
- EM Embolic membrane *sensu* Tanasevitch (2017), not *sensu* Helsdingen (1986) and Hormiga (1994)
- EP Embolus proper *sensu* Saaristo (1971)
- Fe Femur
- MA Median apophysis
- MM Median membrane *sensu* Helsdingen (1965) = embolic membrane *sensu* Helsdingen (1986) and Hormiga (1994)
- Mt Metatarsus
- P Paracymbium
- R Radix
- RA Radical apophysis

T Tegulum
Ti Tibia
TmI Position of trichobothrium on metatarsus I

TAXONOMIC PART

Dumoga Millidge & Russell-Smith, 1992

Type species: *Dumoga arboricola* Millidge & Russell-Smith, 1992.

Dumoga buratino sp. nov.

Figs 1-8, 11-18

Holotype: Male; Indonesia, Sumatra, Jambi Province, Mt Kerinci, footpath to summit, N of Kersik Tua, 1800-1980 m a.s.l., montane rain forest, sifting; 16.II.2000; leg. P. Schwendinger [Sum-00/12].

Paratypes: 1 male, 2 females; collected together with the holotype.

Diagnosis: The new species is characterized by the peculiar shape of its carapace and highly modified palpal tibia in the male, as well as by the rounded dorsal plate of the epigyne in the female.

Etymology: The specific epithet is a noun in apposition, referring to the long-nosed Russian fairy-tale character "Buratino".

Description: *Male (paratype).* Large-sized Erigoninae, total length 3.13, habitus as shown in Fig. 1. Carapace modified (Figs 2-3), 1.65 long, 1.00 wide, reddish brown, with a pale, globular elevation in the middle. Anterior part of carapace protruded forwards, bearing anterior median eyes. Sulci situated at base of central globular outgrowth. Chelicerae 0.63 long, mastidion absent, anterior margin of fang groove with 5 strong teeth. Legs pale reddish brown. Leg I 6.93 long ($1.95+0.35+1.78+1.55+1.30$), leg IV 5.78 long ($1.80+0.28+1.45+1.38+0.87$). Chaetotaxy 2.2.1.1, length of spines about 2 diameters of segment. TmI 0.40. All metatarsi with trichobothrium. Palp (Figs 11-15): Tibia massive, highly modified. Proximal part of paracymbium narrow, middle part with a large rounded outgrowth, distal part hook-shaped. Suprategular apophysis complex, with several outgrowths. Column relatively large, looking like a spongy membranous tissue. Median membrane narrow, protruded forwards. Radix very small, embolus thin, long, making two loops. Abdomen 1.50 long, 1.00 wide, dorsally pale, with several dark spots as shown in Fig. 1.

Female. Total length 2.75, habitus as shown in Fig. 4. Carapace 1.33 long, 1.00 wide, unmodified, reddish brown, with a pale spot in the middle. Chelicerae 0.63 long, anterior margin of fang groove with 5 strong teeth. Legs reddish brown. Leg I 6.34 long

($1.68+0.38+1.65+1.53+1.10$), leg IV 5.18 long ($1.50+0.33+1.35+1.30+0.70$). Chaetotaxy as in male. TmI 0.44. Abdomen 1.50 long, 1.05 wide, dorsal pattern as shown in Fig. 4. Epigyne (Figs 5-8, 16-18) prominent, aperture lacking, dorsal plate rounded, receptacles elongated.

Taxonomic remarks: The new species seems to be most similar to *D. complexipalpis* Millidge & Russell-Smith, 1992, known from males, but clearly differs by the shape of its carapace, by the arrangement of apophyses on the palpal tibia, as well as by the shape of the distal suprategular apophysis.

Distribution: Known only from the type locality on Sumatra Island, Indonesia.

Prosoponoides Millidge & Russel-Smith, 1992

Type species: *Prosoponoides hamatum* Millidge & Russel-Smith, 1992.

Prosoponoides jambi sp. nov.

Figs 9-10, 19-21

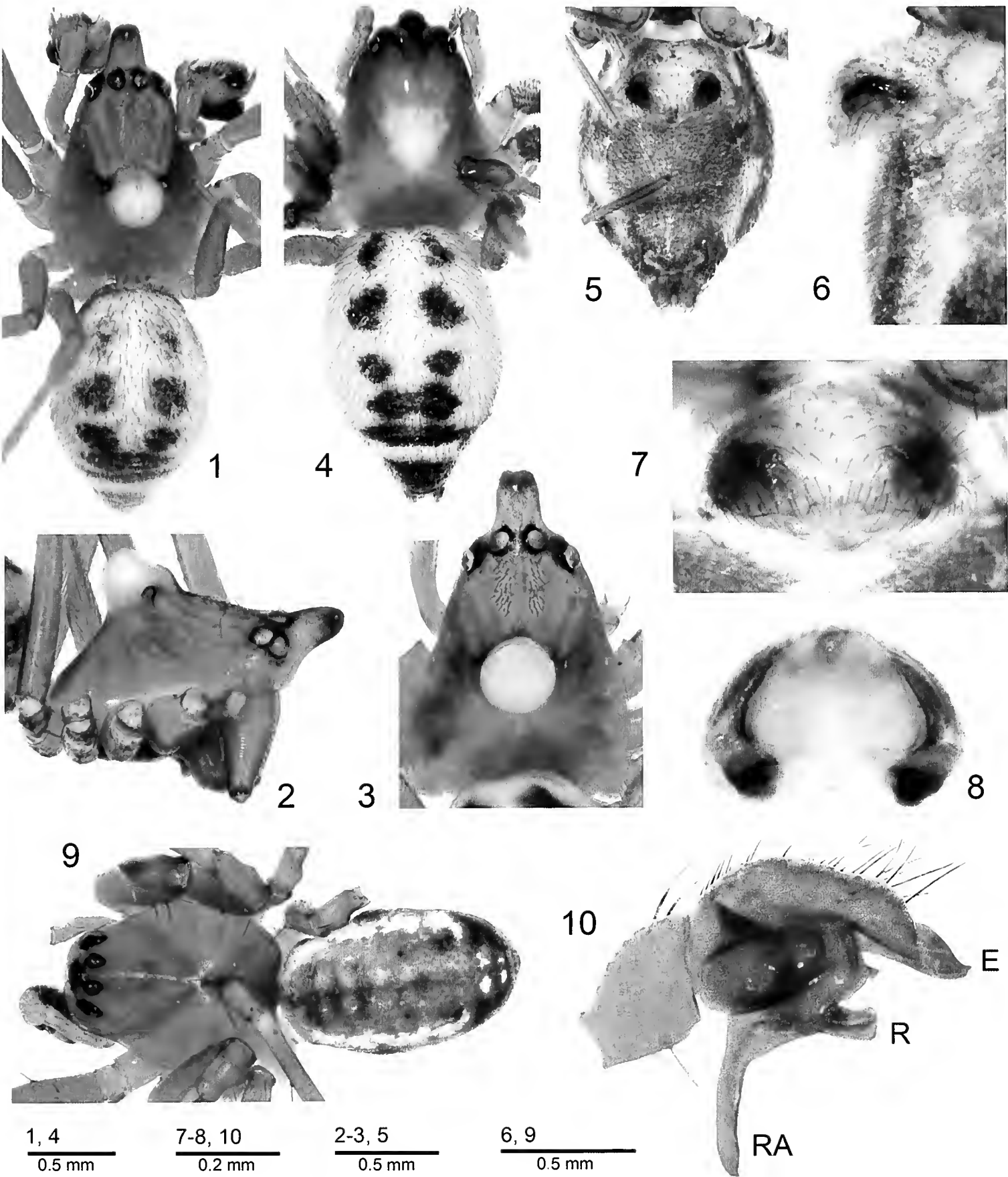
Holotype: Male; Indonesia, Sumatra, Jambi Province, Mt Kerinci, footpath to summit, N of Kersik Tua, 2160 m a.s.l., montane rain forest, sifting; 17.-18. II.2000; leg. P. Schwendinger [Sum-00/13].

Other material examined: MHNG; male holotype of *Prosoponoides hamatum* Millidge & Russel-Smith, 1992. – MHNG; male holotype of *P. simile* Millidge & Russel-Smith, 1992. – MHNG; male holotype of *Kenocymbium deeleanae* Millidge & Russel-Smith, 1992.

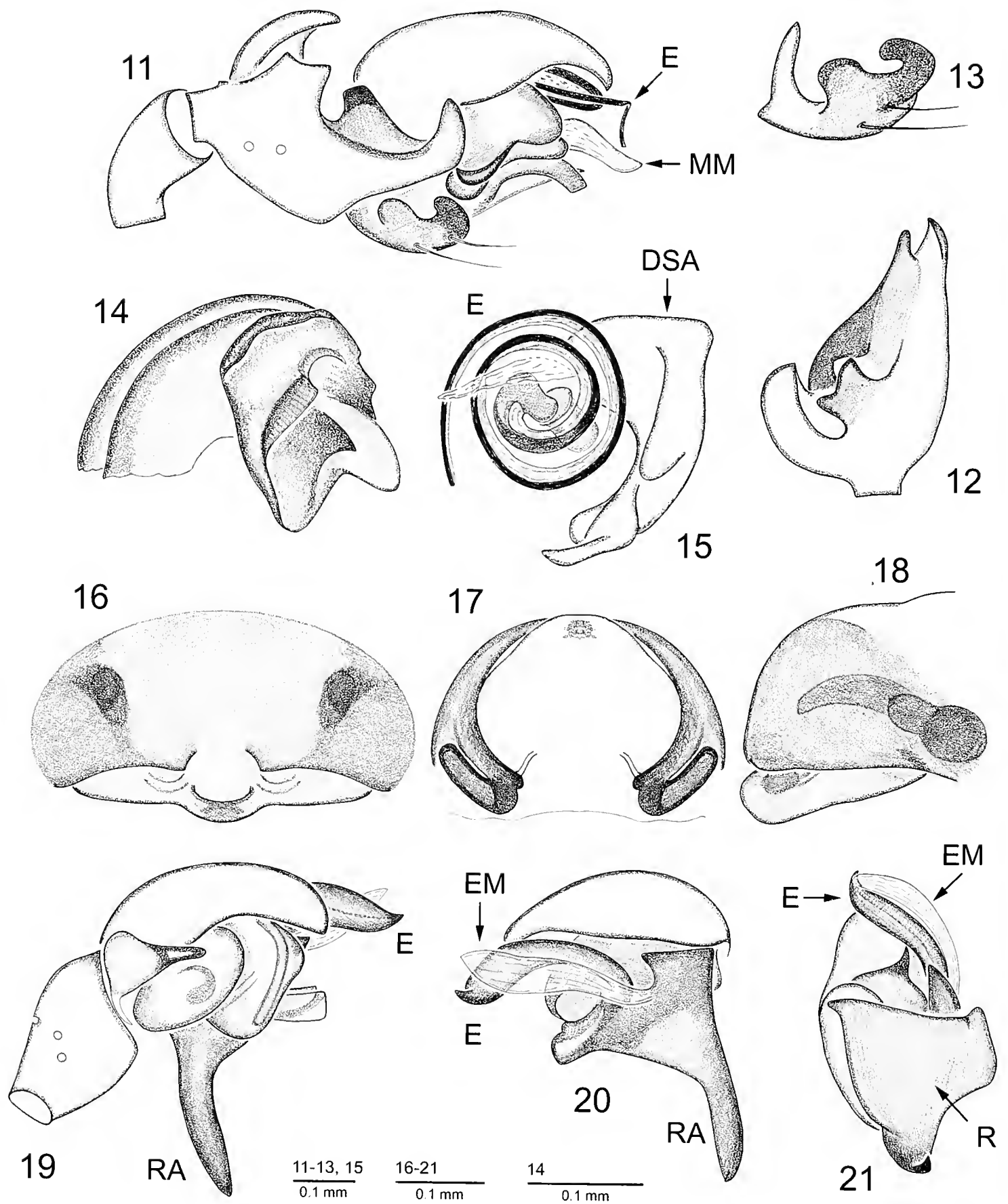
Etymology: The specific epithet is a noun in apposition referring to the "terra typica", the Jambi Province.

Diagnosis: The new species is characterized by the strongly reduced distal part of the paracymbium, by the thick and long embolus, as well as by the presence of a long, downward-directed process on the convector.

Description: *Male (holotype).* Medium-sized Linyphiinae, total length 2.30, habitus as shown in Fig. 9. Carapace 1.05 long, 0.80 wide, unmodified, reddish brown, with darkened cephalic part and indistinct grey radial stripes as well as with darker margin; sulci absent. Chelicerae 0.50 long, mastidion absent. Legs reddish brown, end of segments darkened. Fe I 1.50 long. Leg IV 3.95 long ($1.05+0.25+0.95+1.10+0.60$). Chaetotaxy. FeI: 1-2-0-0, II-IV: 1-0-0-0; TmI: 2-1-1-0, III: 2-0-0-1, IV: 2-1-0-0. TmI 0.22. Metatarsus IV without trichobothrium. Palp (Figs 10, 19-21): Proximal part of paracymbium triangular and projecting forwards, distal part short, narrow, slightly curved, transparent, poorly visible. Distal suprategular apophysis small, claw-shaped.



Figs 1-10. Photographs of *Dumoga buratino* sp. nov., male and female paratypes (1-8), and of *Prosoponoides jambi* sp. nov., male holotype (9-10). (1, 9) Male habitus, dorsal view. (2-3) Male cephalothorax, lateral and dorsal view, respectively. (4) Female habitus, dorsal view. (5-6) Female abdomen, ventral and lateral view, respectively. (7-8) Epigyne, ventral and dorsal view, respectively. (10) Palp, retrolateral view.



Figs 11-21. *Dumoga buratino* sp. nov., male and female paratypes (11-18), and *Prosoponoides jambi* sp. nov., male holotype (19-21). (11, 19) Right palp, retrolateral view. (12) Palpal tibia, dorsal view. (13) Paracymbium. (14) Distal suprategular apophysis. (15) Distal suprategular apophysis and embolic division. (16-18) Epigyne, ventral, dorsal and lateral view, respectively. (20) Cymbium and palpal organ of right palp, prolateral view. (21) Embolic division, ventral view.

Embolus thick, slightly bent. Embolic membrane a long, narrow stripe. Radix large, flat, with a long apophysis directed downwards. Abdomen 1.20 long, 0.70 wide, dorsal pattern as shown in Fig. 9.

Female. Unknown.

Taxonomic remarks: The new species is similar to *Prosoponoides hamatum*, known from northern Sumatra, but clearly differs by a twice shorter distal part of the paracymbium (not shown on palp illustrations of *P. hamatum* in Millidge & Russel-Smith, 1992), as well as by its thick embolus and the presence of a specific process on the convector.

Distribution: Known only from the type locality on Sumatra Island, Indonesia.

Kalimagone gen. nov.

Type species: *Kalimagone cuspidata* sp. nov.

Diagnosis: The new genus belongs to the subfamily Erigoninae and is characterized by the following combination of characters: Medium-sized spiders, total length 1.70–1.95. Chaetotaxy formula 2.2.1.1, trichobothrium on MtIV absent. Male carapace unmodified, sulci absent; chelicerae unmodified, mastidion absent. Distal suprategular apophysis well-developed, protruding far beyond tip of cymbium and bearing a sable-shaped process in the middle. Radix small, embolus long, relatively narrow, directed forwards. The female is characterized by the presence of a median plate on the epigyne, by short seminal ducts and relatively small receptacles situated on both sides of the median plate.

Etymology: The generic name is a combination of two words: “Kalimantan”, the “terra typica”, and a part of the generic name *Erigone*; the gender is feminine.

Species included: *Kalimagone cuspidata* sp. nov. and *K. rotunda* sp. nov.

Taxonomic remarks: The conformation of the male palp of *Kalimagone* gen. nov., namely the presence of a well-developed distal suprategular apophysis, a small radix with a long embolus, a modified palpal tibia, as well as the chaeto- and trichobothriotaxy is similar to that of some representatives of *Gongylidioides* Oi, 1960, especially of *G. keralaensis* Tanasevitch, 2011 and *G. pectinatus* Tanasevitch, 2011, both known from India (Tanasevitch, 2011). The new genus is distinguished from *Gongylidioides* by the absence of a convector (a sclerite in the embolic division which is protecting the embolus), as well as by the structure of the epigyne, namely by the presence of a median plate. The shape of the epigyne resembles that of *Oedothorax* Bertkau in Förster & Bertkau, 1883, but *Oedothorax* species have a totally different conformation of the male palp.

Distribution: Known from Sabah on Borneo Island.

Kalimagone cuspidata sp. nov.

Figs 22–26, 35–41

Holotype: Male; Borneo, East Malaysia, Sabah, West Coast Residency, Kinabalu National Park, Mt Kinabalu, 2590 m a.s.l., misty forest below Layang Layang, plant debris in wet ravine, sifting; 1.V.1987; leg. D. Burckhardt & I. Löbl [#10a].

Paratypes: 2 males, 20 females; collected together with the holotype. – 1 male; Mt Kinabalu, 1750 m a.s.l., Liwagu Trail, rotten wood and other debris along trunk at foot of stump, sifting bark; 27.IV.1987; leg. D. Burckhardt & I. Löbl [#5a]. – 1 male; Mt Kinabalu, 1540 m a.s.l., Liwagu Trail, plant debris in small ravine at foot of old trees, sifting; 29.IV.1987; leg. D. Burckhardt & I. Löbl [#8a].

Diagnosis: This species is characterized by the presence of a short, narrow process on the male palpal tibia, by the apically pointed distal suprategular apophysis in the male, as well as by the rounded receptacula in the female.

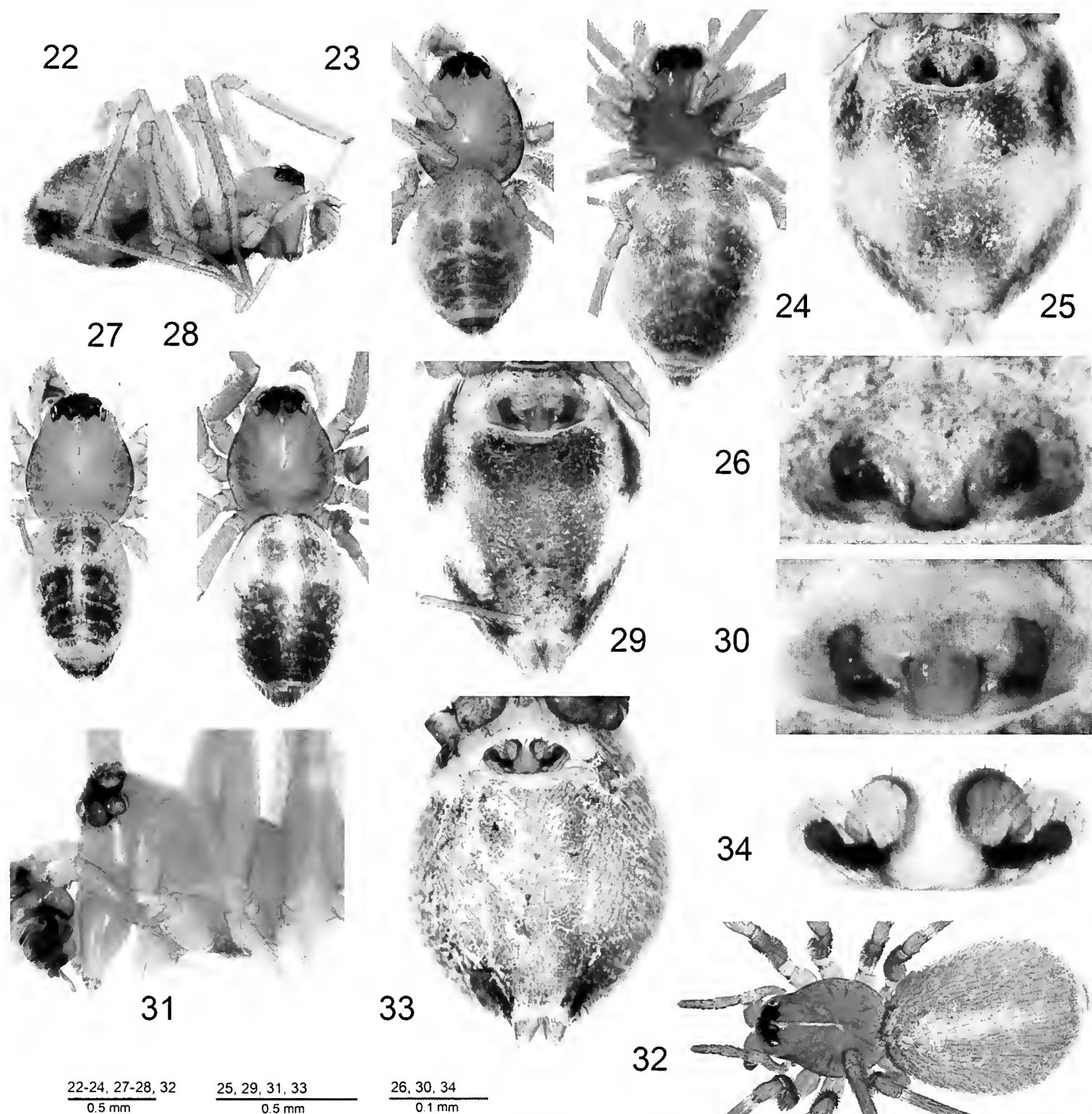
Etymology: The specific epithet is a Latin adjective referring to the shape of the apical part of the distal suprategular apophysis.

Description: *Male (paratype).* Total length 1.75, habitus as shown in Figs 22–23. Carapace unmodified, 0.85 long, 0.68 wide, pale yellow-brown, with indistinct, grey, radial stripes and darker margin; sulci absent. Chelicerae 0.35 long. Legs yellow. Leg I 3.37 long (0.88+0.23+0.88+0.75+0.63), leg IV 3.26 long (0.88+0.20+0.88+0.80+0.50). Chaetotaxy 2.2.1.1, length of spines about 1.5–2 diameters of segment. TmI 0.55. All metatarsi with a trichobothrium. Palp (Figs 35–40): Tibia elongated, ending in a short, narrow process. Paracymbium L-shaped, with a small, sharp tooth in middle part. Tegulum narrowed, pale. Distal suprategular apophysis massive, with a long median apophysis (MA in Figs 36, 40). Radix small, rounded, embolus relatively long and narrow. Abdomen 1.03 long, 0.70 wide, dorsal pattern as shown in Fig. 23.

Female. Total length 1.88, habitus as shown in Fig. 24. Carapace unmodified, 0.88 long, 0.70 wide. Chelicerae 0.35 long. Leg I 3.38 long (1.00+0.25+0.88+0.70+0.55), leg IV 3.33 long (0.95+0.25+0.85+0.80+0.48). Chaetotaxy 2.2.1.1, length of spines about 2–3 diameters of segment. TmI 0.61. Abdomen 1.13 long, 0.75 wide, dorsal and ventral pattern as shown in Figs 24 and 25, respectively. Epigyne (Figs 25–26, 41): median plate with straight or slightly curved lateral edges, receptacles rounded. Carapace and leg coloration as in male.

Taxonomic remarks: The species is similar to its only known congener, *Kalimagone rotunda* sp. nov. (see below).

Distribution: Known only from the type locality in the northeast of Borneo Island.



Figs 22-34. Photographs of *Kalimagone cuspidata* sp. nov., male and female paratypes from Mt Kinabalu (22-26), of *K. rotunda* sp. nov., male holotype and female paratype (27-30), and of *Oedothorax bifoveatus* sp. nov., male and female paratypes from Cibodas Botanical Garden (31-34). (22-23, 27) Male habitus. (31) Male cephalothorax, lateral view. (24, 28, 32) Female habitus. (25, 29, 33) Female abdomen, ventral view. (26, 30, 34) Epigyne, ventral view.

***Kalimagone rotunda* sp. nov.**

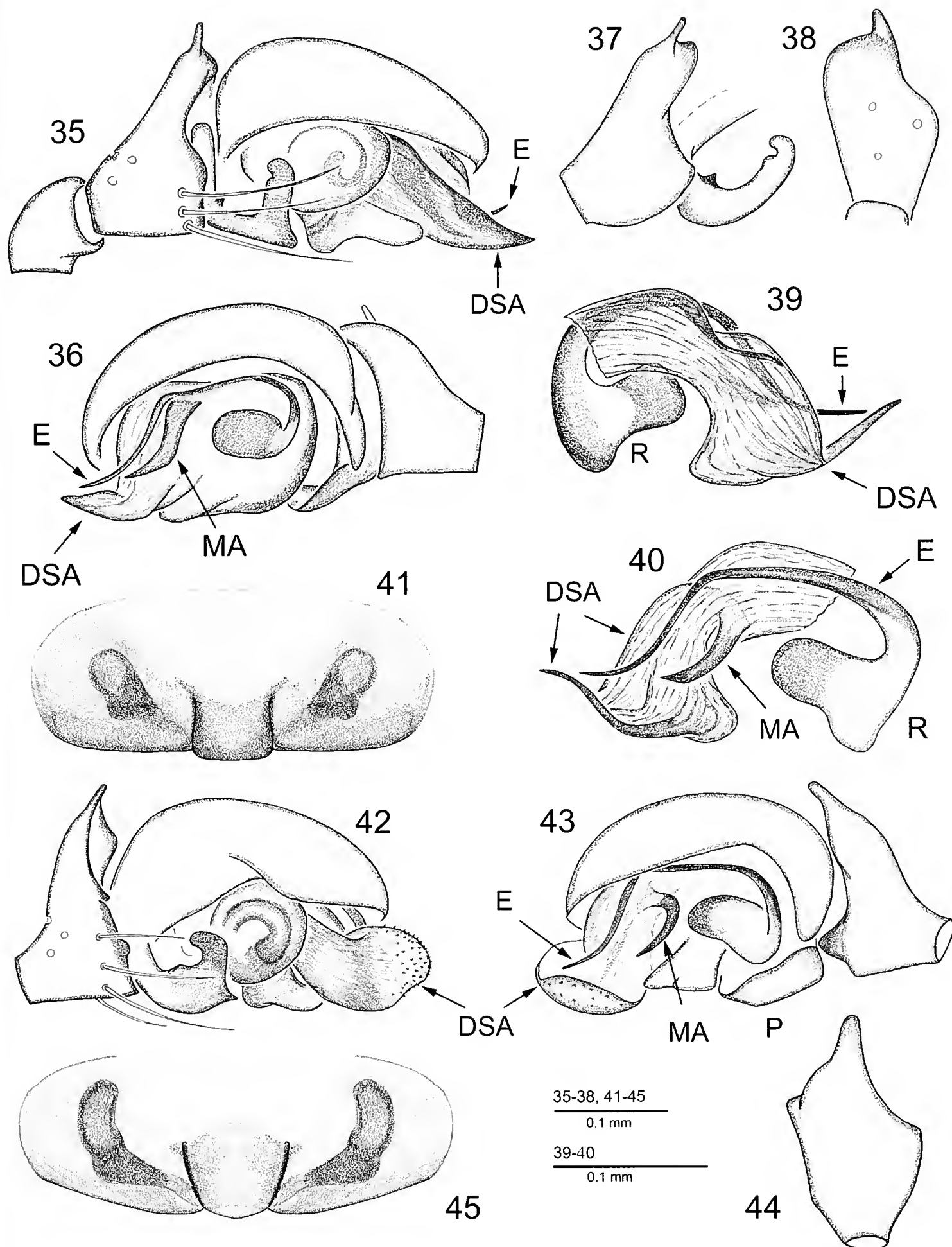
Figs 27-30, 42-45

Holotype: Male; Borneo, East Malaysia, Sabah, Tambunan District, Crocker Range, W slope, ca 1600 m a.s.l., 51-52 km from road Kota Kinabalu to Tambunan, rainforest with *Lithocarpus*, *Castanopsis* and tree ferns, plant debris in wet ravine and at forest edge, sifting; 18.V.1987; leg. D. Burckhardt & I. Löbl [#30a].

Paratypes: 5 females; collected together with the holotype.

Etymology: The specific name is a Latin adjective meaning “rounded”, referring the shape of the distal part of the distal suprategular apophysis.

Diagnosis: The species is characterized by the peculiar shape of the palpal tibia and the rounded distal part of



Figs 35-45. *Kalimagone cuspidata* sp. nov., male and female paratypes from Mt Kinabalu (35-41), and *Kalimagone rotunda* sp. nov., male holotype and female paratype (42-45). (35, 42) Right palp, retrolateral view. (36, 43) Right palp, prolateral view. (37) Palpal tibia and paracymbium, retrolateral view. (38, 44) Palpal tibia, dorsal view. (39-40) Distal suprategular apophysis and embolic division, different aspects. (41, 45) Epigyne, ventral view.

the distal suprategular apophysis in the male, as well as by the bean-shaped receptacles in the female.

Description: *Male (paratype)*. Total length 1.77, habitus as shown in Fig. 27. Carapace unmodified, 0.80 long, 0.65 wide, pale brown, with indistinct, grey, radial stripes and darker margin; sulci absent. Chelicerae long 0.35. Legs yellow. Leg I 3.61 long ($0.95+0.25+0.93+0.85+0.63$), leg IV 3.39 long ($0.90+0.23+0.85+0.88+0.53$). Chaetotaxy 2.2.1.1, length of spines about 1.5-2 diameters of segment. TmI 0.59. All metatarsi with a trichobothrium. Palp (Figs 42-44): Tibia conically elongated. Paracymbium L-shaped. Tegulum small, narrow, pale. Distal suprategular apophysis flat, long and wide, with a claw-shaped median apophysis (MA in Fig. 43). Distal part of distal suprategular apophysis rounded, expanded, carrying tiny denticles, bent apically. Radix small, flat, embolus relatively long and narrow. Abdomen 1.05 long, 0.70 wide, dorsal pattern as shown in Fig. 27.

Female. Total length 1.93, habitus as shown in Fig. 28. Carapace unmodified, 0.78 long, 0.70 wide. Chelicerae 0.35 long. Leg I 3.19 long ($0.88+0.25+0.80+0.73+0.53$), leg IV 3.04 long ($0.88+0.23+0.80+0.70+0.43$). Chaetotaxy 2.2.1.1, length of spines about 2-2.5 diameters of segment. TmI 0.59. Abdomen 1.25 long, 0.78 wide, dorsal and ventral pattern as shown in Figs 28 and 29, respectively. Epigyne (Figs 29-30, 45): median plate with parallel or slightly posteriorly convergent edges, receptacles bean-shaped. Body and leg coloration as in male.

Taxonomic remarks: The species is very similar to *K. cuspidata*, but can easily be distinguished by the rounded, serrate distal part of the distal suprategular apophysis in the male, as well as by the shape of the median plate of the epigyne and the bean-shaped receptacles in the female.

Distribution: Known only from the type locality in the northeast of Borneo Island.

Oedothorax Bertkau in Förster & Bertkau, 1883

Type species: *Oedothorax gibbosus* (Blackwall, 1841).

Remarks: The new species described below is the tenth *Oedothorax* species recorded from the Oriental Realm, and it is the second one known from Southeast Asia, besides *O. convector* Tanasevitch, 2014 (Tanasevitch, 2014b).

Oedothorax bifoveatus sp. nov.

Figs 31-34, 46-51

Holotype: Male; Indonesia, Java, Cibodas Botanical Garden, near Cipanas, ca 50 km E of Bogor, 1400 m a.s.l., vegetational debris in montane *Lithocarpus*

& *Castanopsis* forest, sifting; 3.-6.XI.1989; leg. D. Burckhardt, I. Löbl & D. Agosti [#2a].

Paratypes: 2 males, 17 females; collected together with the holotype. – 1 male, 21 females; Java, Gunung Gede - Pangrango National Park, near Cibodas, 6°47'0"S, 107°01'0"E, 1450-1600 m a.s.l.; 4.-11.V.2005; leg. A. Schulz [AS-05/11]. – 3 males, 1 female; East Malaysia, Borneo Island, Sabah, Tambunan District, Crocker Range, near pass, 1550-1650 m a.s.l., road Kota Kinabalu to Tambunan, *Lithocarpus* & *Castanopsis* forest, sifting dead wood, leaves and moss; 16.V.1987; leg. D. Burckhardt & I. Löbl [#27a].

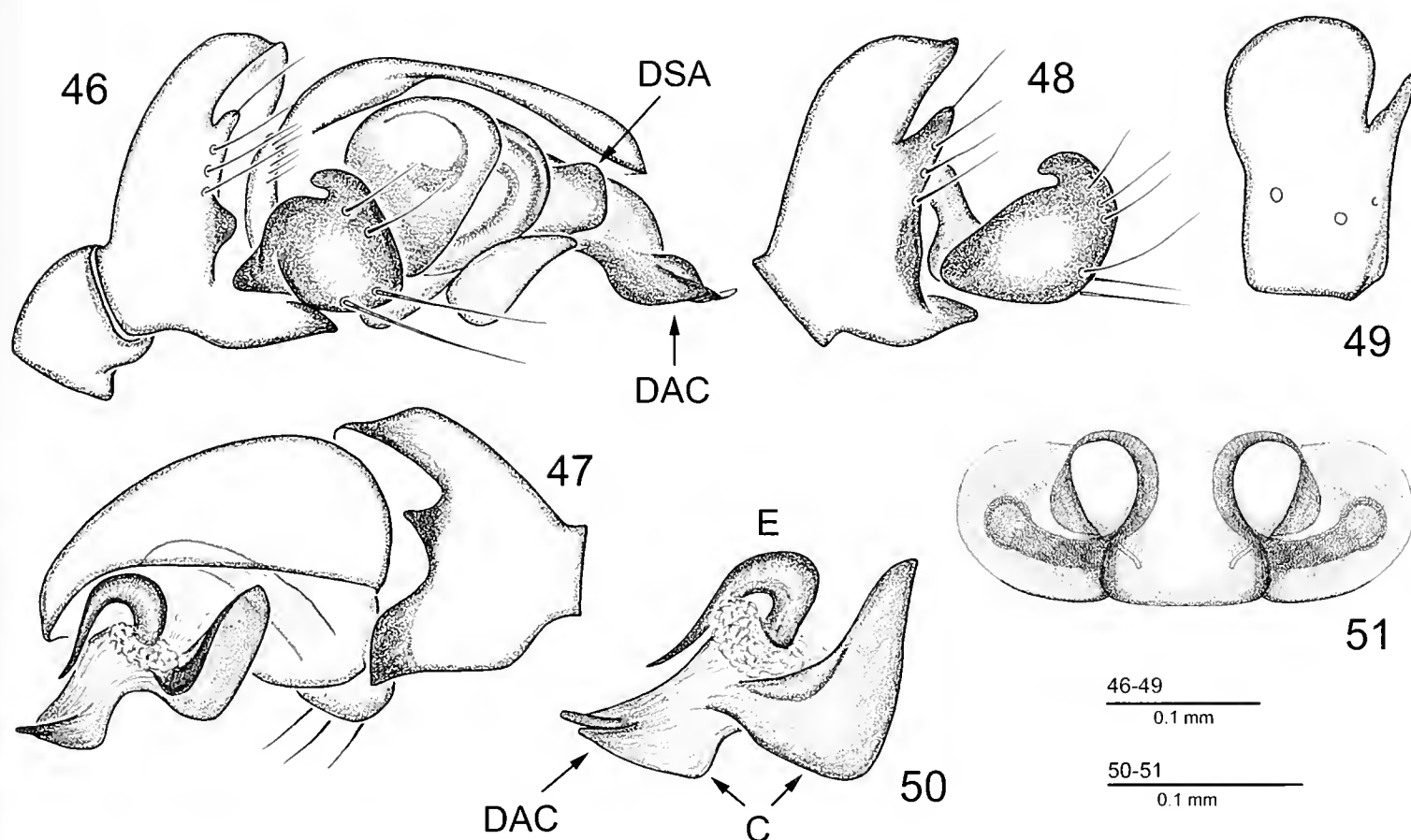
Etymology: The species name is an adjective derived from the Latin "fovea", meaning "a pit", a "socket", referring to the structure of the epigyne.

Diagnosis: The species is characterized by the unmodified carapace, by the peculiar shape of the palpal tibia, as well as by the curved shape of the convector in the male. The female is characterized by the specific structure of the epigyne, namely by the presence of two large sockets on either side of the median plate.

Description: *Male (holotype)*. Total length 1.83. Carapace (Fig. 31) unmodified, 0.95 long, 0.70 wide, greyish pale yellow-brown, with indistinct, grey, radial stripes and darker margin; sulci absent. Chelicerae 0.38 long, mastidion absent. Legs yellow. Leg I 3.43 long ($0.90+0.25+0.88+0.80+0.60$), IV 3.33 long ($0.88+0.25+0.85+0.85+0.50$). Chaetotaxy 2.2.1.1, length of spines about 1-1.5 diameters of segment. TmI 0.61. All metatarsi with trichobothrium. Palp (Figs 46-50): Tibia with a narrow notch retrolaterally and a sharp tooth prolaterally. Paracymbium with a massive distal part, bearing several strong, long spines. Distal suprategular apophysis short and wide. Convector large, spindly curved, distal apophysis (DAC in Figs 46, 50) ending in several short, pointed processes. Abdomen 0.95 long, 0.70 wide, dorsally grey, with a pale, longitudinal stripe.

Female. Total length 2.23, habitus as shown in Fig. 32. Carapace 0.88 long, 0.40 wide, unmodified. Chelicerae 0.40 long. Leg I 3.18 long ($0.88+0.25+0.80+0.75+0.50$), leg IV 3.16 long ($0.88+0.25+0.80+0.75+0.48$). TmI 0.62. Abdomen 1.28 long, 1.00 wide, dorsal and ventral pattern as shown in Figs 32 and 33, respectively. Epigyne (Figs 33-34, 51) with two large rounded sockets on either side of median plate. Receptacles small, rounded. Body coloration, leg coloration and chaetotaxy as in male.

Taxonomic remarks: By the unmodified carapace and by the structure of the embolic division, namely the small embolus and the shape of the convector, the new species resembles several Oriental congeners, e.g., *O. cunur* Tanasevitch, 2015 or *O. rusticus* Tanasevitch, 2015, but is clearly distinguished from those and other



Figs 46-51. *Oedothorax bifoveatus* sp. nov., male and female paratypes from Cibodas Botanical Garden. (46-47) Right palp, retrolateral and prolateral view, respectively. (48) Palpal tibia and paracymbium, retrolateral view. (49) Palpal tibia, dorsal view. (50) Embolic division. (51) Epigyne, ventral view.

congeners by the structure of the epigyne, namely by the presence two large, rounded sockets on either side of the median plate.

Distribution: Known from Borneo Island, East Malaysia, and from Java Island, Indonesia.

Tegulinus gen. nov.

Type species: *Tegulinus sumatranus* sp. nov.

Etymology: The generic name is derived from the Latin “tegulum”, the shape of which is a main character of the genus; the gender is masculine.

Diagnosis: The new genus belongs to the subfamily Erigoninae and is characterized by the following combination of characters: Rather large-sized spiders, total length 1.90-2.25. Chaetotaxy formula 2.2.1.1, all metatarsi with a trichobothrium. Carapace and palpal tibia of males modified; sulci and mastidion absent. Tegulum strongly protruded downwards; distal suprategular apophysis well-developed, long, narrow; embolus small; convector present, simple.

Species included: *Tegulinus sumatranus* sp. nov. and *T. bifurcatus* sp. nov.

Taxonomic remarks: The taxonomic position of

this new genus is unclear, especially as the female is unknown. The conformation of the embolic division, namely the shape of the small embolus and the structure of the convector, somewhat resembles that of some Oriental species of *Oedothorax* Bertkau in Förster & Bertkau, 1883, e.g., *O. meghalaya* Tanasevitch, 2015 or *O. stylus* Tanasevitch, 2015. The discovery of congeneric females and/or other representatives of *Tegulinus* gen. nov. should clarify the position of the genus among the Erigoninae.

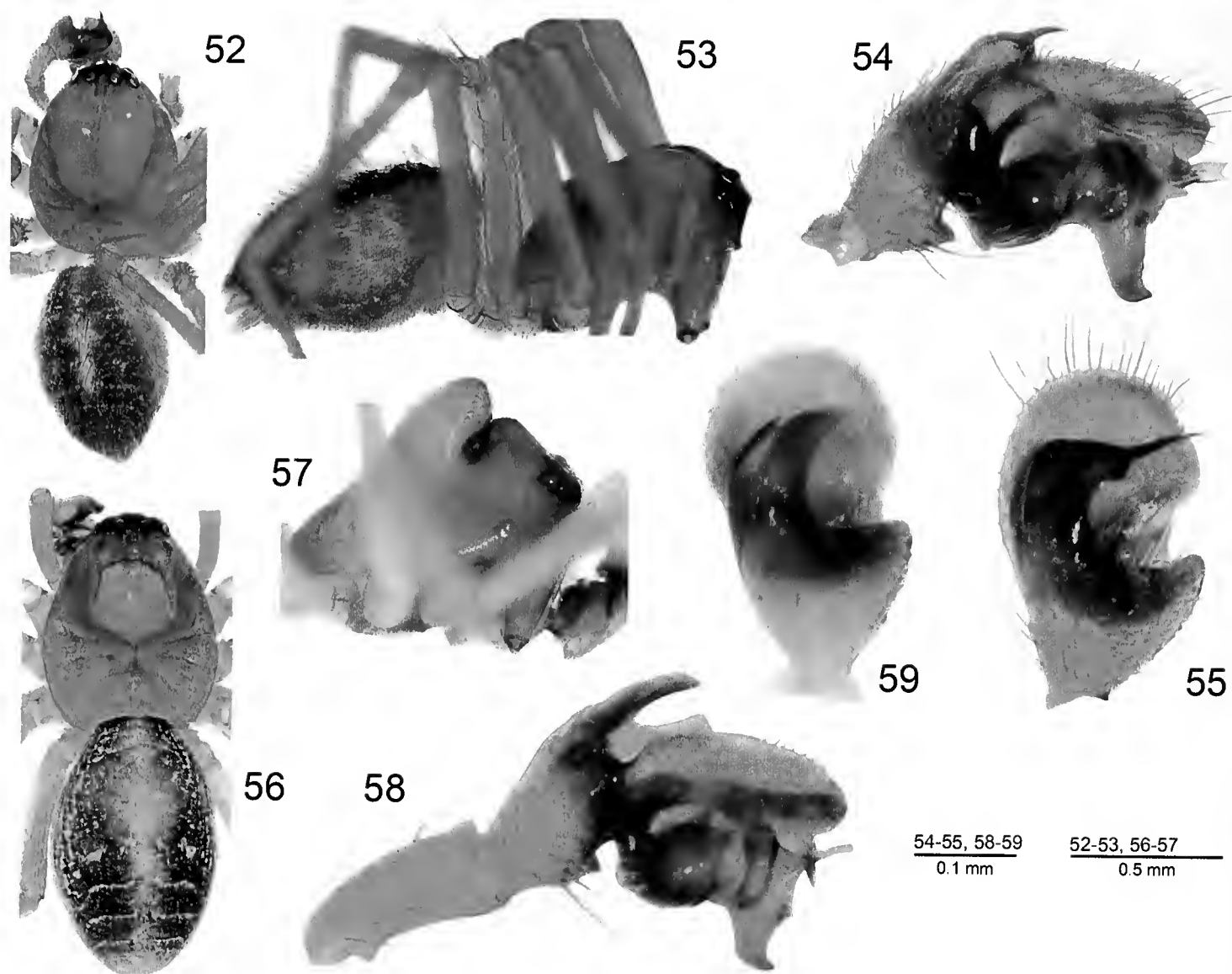
Distribution: Known only from Sumatra Island, Indonesia.

Tegulinus sumatranus sp. nov.

Figs 52-55, 60-64

Holotype: Male; Indonesia, Sumatra, Jambi Province, Mt Kerinci, 3300 m a.s.l., low Ericaceae scrub, sifting of vegetational debris; 12.XI.1989; leg. D. Burckhardt, I. Löbl & D. Agosti [#12a].

Paratypes: 1 male; collected together with the holotype. – 1 male; Mt Kerinci, 2100 m a.s.l., vegetational debris, transition upper montane *Lithocarpus* & *Castanopsis* to moss forest, sifting; 14.XI.1989; leg. D. Burckhardt, I. Löbl & D. Agosti



Figs 52-59. Photographs of *Tegulinus sumatranus* sp. nov., male paratype from Mt Tujuh (52-55), and of *T. bifurcatus* sp. nov., male holotype (56-59). (52-53, 56) Habitus. (57) Cephalothorax, lateral view. (54, 58) Right palp, retrolateral view. (55, 59) Palpal tibia, dorsal view.

[#16]. – 1 male; Mt Kerinci, footpath to summit, N of Kersik Tua, 1800-1980 m a.s.l., montane rain forest, sifting; 16.II.2000; leg. P. Schwendinger [Sum-00/12]. – 3 males; Mt Kerinci, footpath to summit, N of Kersik Tua, 2160 m a.s.l., montane rain forest, sifting; 17.-18. II.2000; leg. P. Schwendinger [Sum-00/13]. – 2 males; Jambi Province, Mt Tujuh, footpath to Lake Mt Tujuh, 1500-2000 m a.s.l., montane rain forest; 20.II.2000; leg. P. Schwendinger [Sum-00/15].

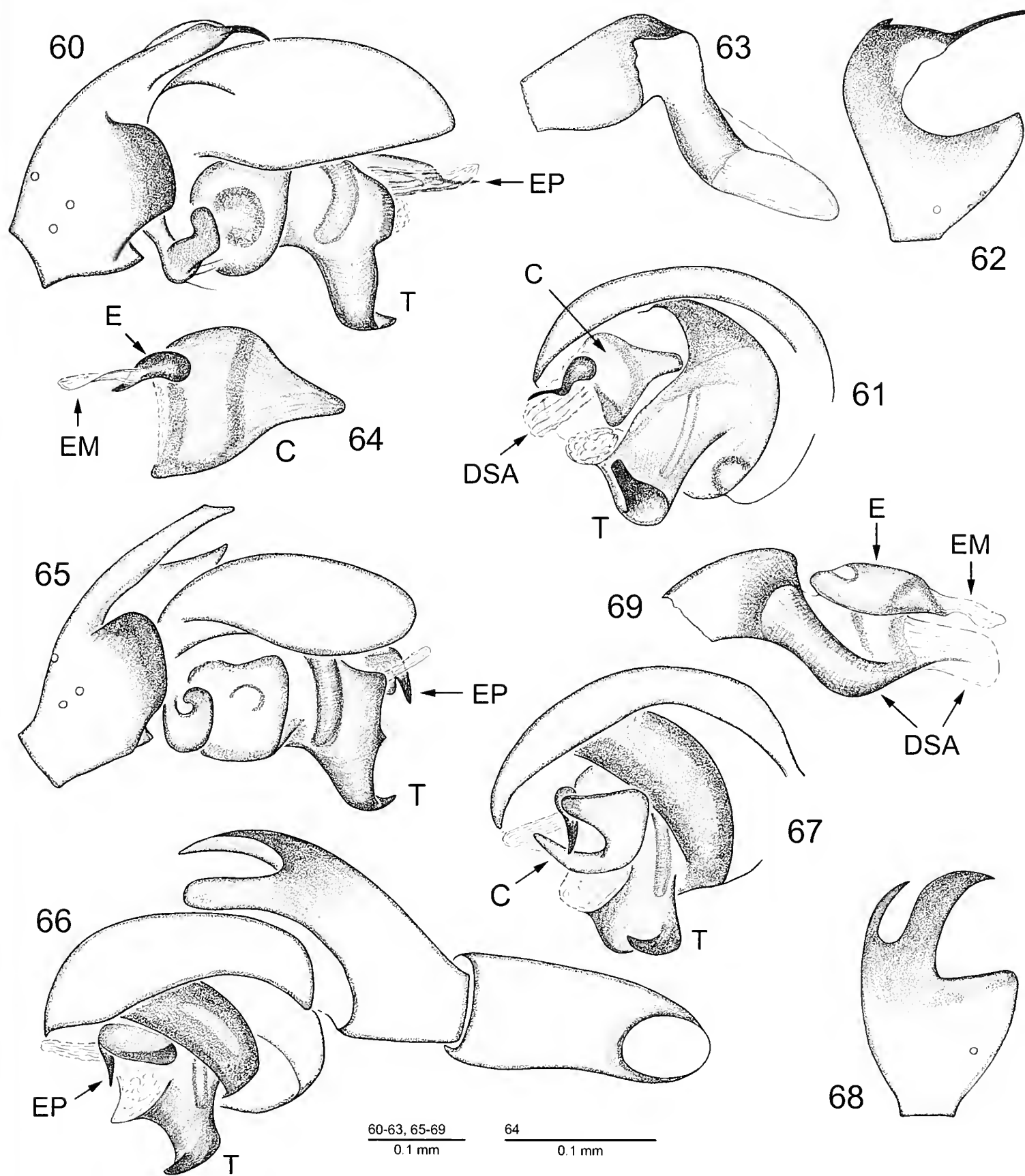
Etymology: The specific epithet, an adjective, refers to the “terra typica”, Sumatra Island.

Diagnosis: The species is characterized by the weakly modified carapace, and the presence of a specific process on the palpal tibia.

Description: *Male* (paratype from Mt Tujuh). Total length 2.15, habitus as shown in Figs 52-53. Carapace (Fig. 53) 1.05 long, 0.75 wide, pale yellow-

brown, convex dorsally, with indistinct, grey, radial stripes posteriorly; sulci absent. Chelicerae 0.38 long, mastidion absent. Legs yellow. Leg I 3.52 long ($1.00+0.28+0.88+0.83+0.53$), leg IV 3.34 long ($0.95+0.25+0.78+0.88+0.48$). Chaetotaxy 2.2.1.1, length of spines about 1.5-2 diameters of segment. TmI 0.77. All metatarsi with trichobothrium. Palp (Figs 54-55, 60-64): Tibia with a wide apophysis ending in a long, narrow, spear-like process. Paracymbium L-shaped, its distal part bearing several spines. Tegulum conical, strongly protruded downwards, pointed and bent apically. Distal suprategular apophysis relatively long, its distal part almost transparent. Convector relatively wide, triangular. Embolus small, comma-shaped, embolic membrane narrow, moderately sclerotized. Abdomen 1.00 long, 0.75 wide, dorsal pattern as shown in Fig. 52.

Female. Unknown.



Figs 60-69. *Tegulinus sumatranus* sp. nov., male paratype from Mt Tujuh (60-64), and *T. bifurcatus* sp. nov., male holotype (65-69). (60, 65) Right palp, retrolateral view. (61, 66, 67) Right palp, prolateral view. (62, 68) Palpal tibia, dorsal view. (63) Distal suprategular apophysis. (64) Embolic division. (69) Distal suprategular apophysis and embolus.

Taxonomic remarks: The new species is similar to its only known congener, *Tegulinus bifurcatus* sp. nov. (see below).

Distribution: Known only from two localities in the mountains of Jambi Province, Sumatra Island, Indonesia.

Tegulinus bifurcatus sp. nov.
Figs 56-59, 65-69

Holotype: Male; Indonesia, Sumatra, Jambi Province, Mt Kerinci, 3000 m a.s.l., 12.XI.1989; leg. D. Agosti, D. Burckhardt & I. Löbl [#13a].

Diagnosis: The species is characterized by the presence of a hump on the carapace, by the presence of two processes on the palpal tibia, as well as by the relatively small convector.

Etymology: The specific name is a Latin adjective referring to the shape of the male palpal tibia.

Description: *Male (holotype).* Total length 1.90, habitus as shown in Fig. 56. Carapace 0.90 long, 0.73 wide, pale brown, with a pale, rounded hump in the centre (Figs 56-57). Chelicerae 0.30 long, mastidion absent. Legs yellow. Leg I 2.96 long (0.85+0.25+0.70+0.68+0.48.), leg IV 2.93 long (0.80+0.23+0.70+0.75+0.45). Chaetotaxy unknown, spines lost. TmI 0.80. All metatarsi with trichobothrium. Palp (Figs 58-59, 65-69): Dorso-apical process of tibia divided into two branches.

Paracymbium small, L-shaped. Tegulum conical, strongly protruded downwards, pointed and bent apically. Distal suprategular apophysis small, ending in a narrow, almost transparent process. Convector with a deep hollow. Embolus small, comma-shaped. Abdomen 1.00 long, 0.75 wide, dorsal pattern as shown in Fig. 56. *Female.* Unknown.

Taxonomic remarks: The new species is similar to its only known congener, *T. sumatranus* sp. nov., but can be easily distinguished by the presence of a hump on the carapace and of two processes on the palpal tibia (*versus* only one in *T. sumatranus* sp. nov.).

Distribution: Known only from the type locality at high altitudes in Jambi Province, Sumatra Island, Indonesia.

BIOGEOGRAPHICAL PART

In Table 1 I give an overview of the occurrence of linyphiid spiders on Borneo, Sumatra, Java and continental SE-Asia. According to that, the fauna of these islands is not as poor in species as we previously thought and shows a high degree of presumed endemism. Among the 58 species listed, only 12 were recorded from continental Southeast Asia. Only one species, *Kaestneria bicultrata*, is also known from outside that region (southern China), and one species, *Ostearius melanopygius*, is a cosmopolite. The remaining species are presumably local or regional endemics.

Table 1. Occurrence of linyphiid spiders on Borneo, Sumatra, Java and in continental Southeast Asia, including new data.

Species	Borneo	Sumatra	Java	Continental SE Asia
<i>Bathypantes minor</i> Millidge & Russell-Smith, 1992	+			
<i>B. paracymbialis</i> Tanasevitch, 2014a		+		+
<i>Batueta baculum</i> Tanasevitch, 2014b	+	+		+
<i>Caenonetria perdita</i> Millidge & Russell-Smith, 1992	+			
<i>C. orientalis</i> Locket, 1982			+	+
<i>Dendronetria humilis</i> Millidge & Russell-Smith, 1992	+			
<i>D. obscura</i> Millidge & Russell-Smith, 1992	+			
<i>Dubiaranea deelemanae</i> Millidge, 1995	+			
<i>Dumoga buratino</i> sp. nov.		+		
<i>Enguterothrix simpulum</i> (Tanasevitch, 2014b)	+			+
<i>Eordea bicolor</i> Simon, 1899		+		
<i>Erigone bifurca</i> Locket, 1982		+		+
<i>Erigophantes borneoensis</i> Wunderlich, 1995	+			
<i>Helsdingenia hebesoides</i> Saaristo & Tanasevitch, 2003a		+		
<i>Indophantes barat</i> Saaristo & Tanasevitch, 2003b		+		
<i>I. kalimantanus</i> Saaristo & Tanasevitch, 2003b	+			

<i>I. kinabalu</i> Saaristo & Tanasevitch, 2003b	+			
<i>I. lehtineni</i> Saaristo & Tanasevitch, 2003b	+			
<i>I. sumatera</i> Saaristo & Tanasevitch, 2003b		+		
<i>Kaestneria bicultrata</i> Chen & Yin, 2000		+		
<i>Kalimagone cuspidata</i> sp. nov.	+			
<i>K. rotunda</i> sp. nov.	+			
<i>Kenocymbium deelemanae</i> Millidge & Russell-Smith, 1992		+		+
<i>Ketambea permixta</i> Millidge & Russell-Smith, 1992			+	
<i>K. rostrata</i> Millidge & Russell-Smith, 1992		+		
<i>K. vermiformis</i> Millidge & Russell-Smith, 1992			+	
<i>Knischatiria longispina</i> Wunderlich, 1995		+		
<i>Linyphia phyllophora</i> Thorell, 1890		+		
<i>Locketiella parva</i> Millidge & Russell-Smith, 1992	+			
<i>Locketina fissivulva</i> (Millidge & Russell-Smith, 1992)	+			
<i>L. pusilla</i> (Millidge & Russell-Smith, 1992)	+			
<i>Metalephyphantes kraepelini</i> (Simon, 1905)			+	
<i>Mitrager noordami</i> Helsdingen, 1985b			+	
<i>Nasootia asocialis</i> (Wunderlich, 1974)			+	
<i>N. crucifera</i> (Thorell, 1895)	+			
<i>Nasoonaria sinensis</i> Wunderlich, 1995		+		
<i>Nematogmus asiaticus</i> Tanasevitch, 2014a		+		
<i>N. dentimanus</i> Simon, 1886			+	
<i>Neriere amiculata</i> (Simon, 1905)			+	
<i>N. beccarii</i> (Thorell, 1890)		+		
<i>N. macella</i> (Thorell, 1898)		+	+	
<i>N. strandia</i> (Blauvelt, 1936)	+			
<i>N. sundaica</i> (Simon, 1905)			+	
<i>Oedothorax bifoveatus</i> sp. nov.	+		+	
<i>Ostearius melanopygius</i> (O. Pickard-Cambridge, 1880)	+			+
<i>Phyllarachne levicula</i> Millidge & Russell-Smith, 1992	+			
<i>Piesocalus javanus</i> Simon, 1894			+	
<i>Plectemبولus quadriflectus</i> Millidge & Russell-Smith, 1992	+	+		+
<i>P. quinquefectus</i> Millidge & Russell-Smith, 1992		+		+
<i>P. similis</i> Millidge & Russell-Smith, 1992		+		
<i>Pronasootia sylvatica</i> Millidge, 1995	+			
<i>Prosoponoides hamatus</i> Millidge & Russell-Smith, 1992		+		+
<i>P. jambi</i> sp. nov.		+		
<i>P. kaharianus</i> Millidge & Russell-Smith, 1992	+			
<i>Tapinopa vara</i> Locket, 1982		+		+
<i>Tegulinus bifurcatus</i> sp. nov.		+		
<i>T. sumatranus</i> sp. nov.		+		
<i>Theoa hamata</i> Tanasevitch, 2014a		+		+
Total species	24	26	12	12

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Distribution et statut du Rat des moissons (*Micromys minutus*) dans le bassin genevois

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Résumé : Des prospections actives et ciblées ont été menées entre 2014 et 2016 dans l'espoir de trouver d'éventuelles populations résiduelles de Rats des moissons (*Micromys minutus*) dans le bassin genevois. Après avoir repéré une soixantaine de sites favorables à l'espèce, des recherches de nids ont été effectuées ainsi que des piégeages. Ces recherches ont permis de trouver 12 nouvelles stations, toutes situées dans le Pays de Gex (France, Ain), et de présumer que l'espèce est aujourd'hui absente du canton de Genève et peut-être aussi de la partie haut-savoyarde du Bas-Chablais située dans la zone prospectée. Ces découvertes révèlent le niveau de menace important qui pèse sur presque toutes les populations de Rats des moissons du bassin genevois.

Mots-clés : Rat des moissons - magnocariçaie - bassin genevois - Pays de Gex - nids - piégeage.

Abstract : Distribution and status of the Harvest Mouse (*Micromys minutus*) in the Geneva Basin. - Targeted active surveys were conducted between 2014 and 2016 in order to find residual Harvest Mouse (*Micromys minutus*) populations in the Geneva Basin. After locating approximately 60 potentially favourable sites for the species, nest searches and trapings were carried out. These searches permitted to identify 12 new occupied sites, all located in Pays de Gex (France, Ain). It must be assumed that today the species is no longer present on the territory of the canton of Geneva as well as the lower region of the Chablais (France, Haute-Savoie). These observations demonstrate that most Harvest Mouse populations of the Geneva Basin are under a high level of threat.

Keywords : Harvest Mouse - Magnocaricion - Geneva Basin - Pays de Gex - nest - trapping.

INTRODUCTION

Le Rat des moissons *Micromys minutus* (Pallas, 1771) possède une aire de distribution très large, qui s'étend du nord de l'Espagne jusqu'au Japon, et, à l'exception du Vietnam (Abramov *et al.*, 2009), ne révèle à ce jour que très peu de divergences génétiques au sein de ses diverses populations (Yasuda *et al.*, 2005). De fait, il n'est pas considéré comme une espèce menacée au niveau mondial. En revanche, plusieurs études ont clairement mis en évidence son déclin au cours des quatre dernières décennies dans plusieurs régions d'Europe, notamment en Angleterre, en Suisse et dans certaines régions de France (Meek, 2011 ; Blant *et al.*, 2012 ; Lardelli, 1981 ; Butet & Paillat, 1998 ; Mitchell-Jones *et al.*, 1999). En Suisse, sa présence est aujourd'hui confinée sur la rive sud du lac de Neuchâtel, aux marais de la Versoix (canton de Vaud), à quelques zones marécageuses du canton du Jura, ainsi que dans les environs de Bâle et de Schaffhouse ; présent autrefois non loin du lac de Constance et dans le canton

du Tessin, il n'y a plus été retrouvé depuis (Maddalena & Zanini, 2008). Aujourd'hui, seules les populations des marais de la Versoix et du lac de Neuchâtel paraissent viables sur le long terme (Vogel & Gander, 2014).

En ce qui concerne son statut dans le bassin genevois au cours de ces deux derniers siècles, les rares informations disponibles ne permettent pas d'affirmer si l'espèce était fréquente à un moment ou à un autre de cette période. En effet, les seules données certaines et antérieures à 2000 se rapportent à trois nids trouvés par Aellen et Strinati en 1966 dans la région de Bogis-Bossey (canton de Vaud) et conservés au Muséum de Genève, à une mâchoire trouvée dans une pelote de réjection en provenance de l'Etournal, dans le département de l'Ain (Bordon, comm. pers.), à une observation visuelle faite au marais du Grand Bataillard (Blant *et al.*, 2012), ainsi qu'à des restes osseux trouvés entre 1966 et 1968 dans des pelotes de réjection d'Effraie des clochers (*Tyto alba*) en provenance de Bogis-Bossey et de Founex, dans le canton de Vaud (données du Centre suisse de cartogra-

phie de la faune, Neuchâtel). A ces données, vient encore s'ajouter une observation de nid faite au Moulin-de-Vert (canton de Genève) par un garde de l'environnement il y a un peu moins d'une vingtaine d'années, observation qui n'a pas pu être confirmée (Blant *et al.*, 2012) et qui pourrait se rapporter à un nid de Muscardin (*Muscardinus avellanarius*). Par ailleurs, d'autres données issues de restes osseux trouvés dans des pelotes de réjection font état de la présence de l'espèce en 1982 à la Gara, près de Jussy, et en 1991, à Meyrin (canton de Genève), ainsi qu'au Mont de Sion en 1969 (Haute-Savoie). Toutefois, le matériel ayant servi aux identifications n'ayant pas été retrouvé pour confirmation, ces dernières données doivent être prises avec une certaine réserve (Morel, comm. pers.). Il en va de même avec trois nids des collections du Muséum de Genève collectés par Schauenberg à l'avenue d'Aïre (canton de Genève) en 1945, dont l'état de conservation ne permet pas de confirmer s'ils sont les œuvres de Rats des moissons ou de Muscardins. Enfin, signalons que Hainard affirmait que l'espèce manquait «à notre région» et que Fatio, dans son ouvrage sur les mammifères de la Suisse, n'a pas rapporté la présence de l'espèce dans le canton de Genève, ni même dans le bassin genevois, en ajoutant néanmoins avoir «trouvé le Rat nain sur le territoire français, non loin de nous, mais au delà du Fort de l'Ecluse et par conséquent en dehors de nos limites naturelles» (Hainard, 1949; Fatio, 1869). Concernant la période postérieure à 2000, aucune donnée suffisamment documentée ne permettait avant ces présentes recherches de mettre en évidence l'existence certaine du Rat des moissons dans le bassin genevois, hormis dans le complexe franco-suisse des marais de la haute Versoix (Marchesi & Descombes, 2008). Toutefois, selon Faugier et Bulliffon (2015), qui ne mentionnent aucune source et aucune localité, l'espèce serait présente à l'est et à l'extrême nord du département de la Haute-Savoie près du lac Léman.

Devant ce déficit d'informations et la confirmation récente de la présence d'une importante population de Rats des moissons au marais du Grand Bataillard, situé au bord de la Versoix dans le canton de Vaud (Marchesi & Descombes, 2008), il a été décidé de rechercher activement l'espèce dans tout le bassin genevois afin de retrouver d'éventuelles populations résiduelles, sachant que jusque vers le début du XX^e siècle de très grandes zones marécageuses ou prairiales subsistaient encore en maints endroits de la zone étudiée.

ZONE D'ÉTUDE

La zone d'étude constitue une entité territoriale franco-suisse relativement cohérente d'un point de vue biogéographique. Elle regroupe la totalité du canton de Genève, l'extrême sud-ouest du canton de Vaud, le Pays de Gex (Ain) et une partie de l'extrémité occidentale du Bas-Chablais haut-savoyard. Les limites de cet espace géographique sont délimitées au nord par une ligne partant

de Saint-Cergue (Vaud) et suivant plus au sud-est la Promenthouse, au nord-ouest par la ligne de crête de la chaîne du Jura, au sud par celle du Vuache et du pli du Mont-de-Sion, puis à l'est par celle des Voirons et enfin par le Redon, rivière se jetant dans le Léman à la hauteur de Séchex (Fig. 1). La superficie du bassin genevois ainsi circonscrite est de 1032 km², les deux tiers environ se trouvant sur France (642 km²), un peu moins d'un quart sur le canton de Genève (282 km²) et le reste sur le canton de Vaud (108 km²).

MATÉRIEL ET MÉTHODES

A l'instar de la plupart des petits rongeurs, le Rat des moissons n'est pas une espèce facile à observer visuellement, même si ses activités sont en partie diurnes (Rahm, 1995; Cross, 1970). En France, sa distribution géographique est d'ailleurs essentiellement connue par l'analyse des pelotes de réjection de rapaces, surtout celles de l'Effraie des clochers (Quéré & Le Louarn, 2011), ce qui ne permet pas, il va sans dire, une localisation exacte des populations. En outre, il s'est avéré que les critères d'identification des crânes posent parfois des problèmes aux naturalistes inexpérimentés et qu'il existe de ce fait, selon Blant *et al.* (2012), des risques de confusion avec la Souris domestique (*Mus domesticus*). Par conséquent, il est nécessaire d'entreprendre des recherches avec d'autres méthodes indirectes. Aussi, sachant que dans nos régions l'espèce est essentiellement inféodée à des milieux humides présentant une végétation dense de hautes plantes herbacées (Darinot & Favier, 2014; Blant *et al.*, 2012), généralement des magnocariçaies, mais également des phalaridaies et des prairies hygrophiles ou mésohygrophiles, des premières recherches ont été effectuées dans plusieurs zones du bassin genevois déjà connues pour abriter des formations végétales susceptibles de convenir au Rat des moissons. Des prospections ont alors été entreprises en 2014 et 2015 dans une quinzaine de sites, ce qui a permis de détecter la présence de l'espèce dans deux stations du Pays de Gex (marais de l'Etournel et de Prodon). Fort de ce résultat, des recherches à partir de cartes topographiques et de photographies aériennes antérieures à 1960 ont été ensuite réalisées en 2016 afin de localiser les emplacements d'anciennes zones marécageuses ou prairiales situées en dessous de 700 m d'altitude, ceci en raison des préférences de l'espèce, du moins dans nos régions, pour des stations situées essentiellement à l'étage collinéen (Rahm, 1995; Butet & Paillat, 1998; Quéré & Le Louarn, 2011). Puis, chaque secteur a été visité dans l'espoir de trouver des milieux favorables à l'espèce, comme des cariçaies, des prairies sur sol hydromorphe, des friches humides, voire des canaux de drainage bordés de végétation herbacée suffisamment haute pour abriter une population résiduelle de Rats des moissons. Enfin, des recherches plus approfondies ont été entreprises sur une bonne soixantaine de sites du bassin genevois, parmi

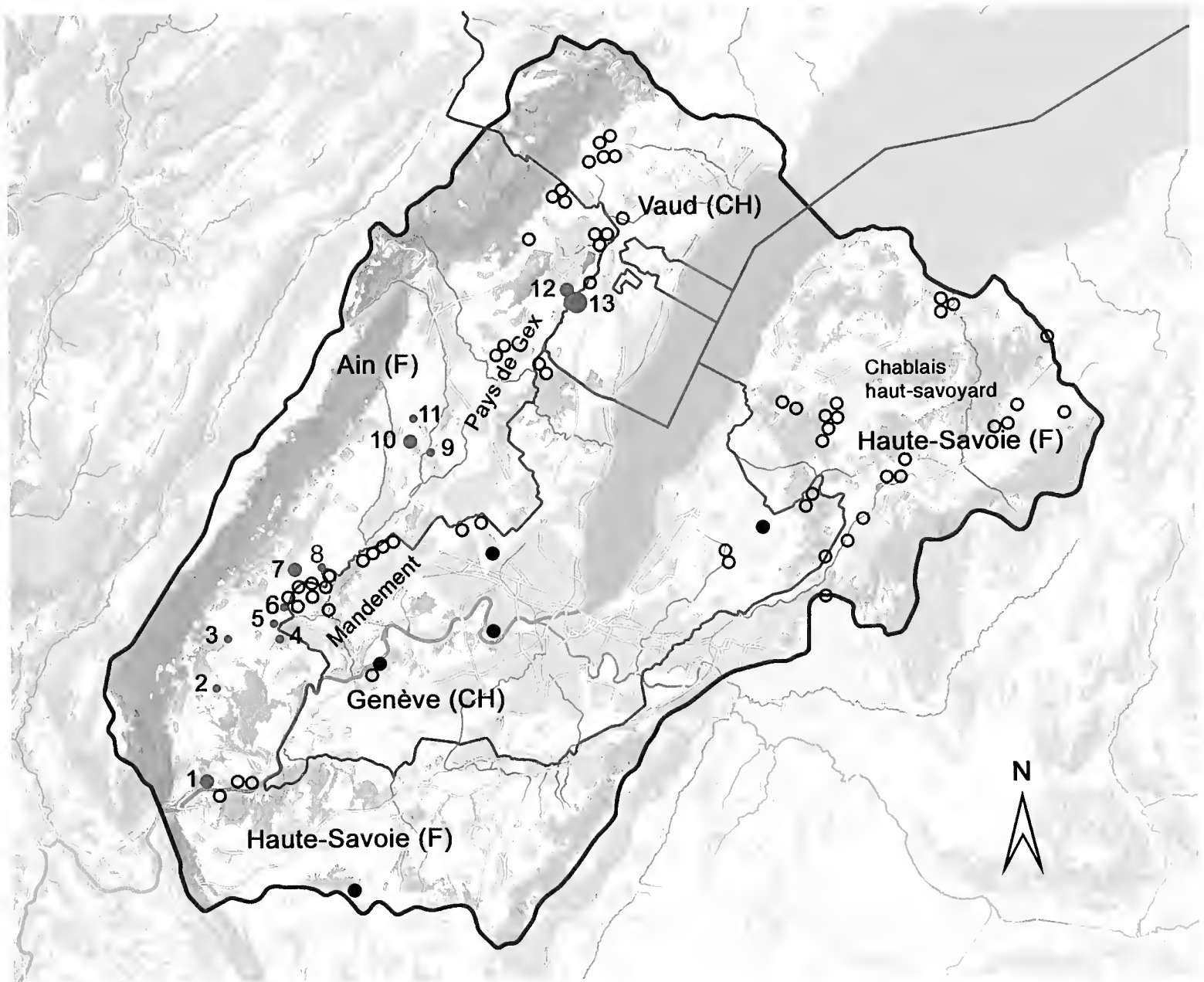


Fig. 1. Localisation géographique des sites prospectés avec ou sans succès dans le bassin genevois (délimité par un trait vert). Les points rouges indiquent les nouvelles stations, le point bleu celle du Bataillard (connue depuis 1966), les points noirs les stations historiques mais douteuses et les cercles les sites prospectés sans succès. La taille des points indique une première évaluation des menaces qui pèsent sur les populations; grand point: peu menacée (protection efficace), point moyen: menacée (renforcement nécessaire des mesures de protection), petit point: très menacée (mesures de protection urgentes à engager).

lesquels une petite friche à Molinie (*Molinia arundinacea*) située à Greny sur la commune de Péron (Ain), site où la découverte fortuite en septembre 2016 d'un nid présumé de Rat des moissons par une botaniste a permis de localiser une petite population (Fig. 2).

Les preuves de présence de Rats des moissons dans les sites retenus ont été essentiellement obtenues par la recherche de ses petits nids sphériques suspendus invariablement dans la haute végétation herbacée et très souvent dans des formations de grandes laïches (Magnocaricion), comme *Carex acutiformis*. Soulignons ici que ces nids peuvent être parfois confondus avec ceux du Muscardin qui fréquente volontiers les phragmitaies et certaines zones marécageuses envahies par une végétation ligneuse pionnière. Il est pour cela nécessaire de vérifier si les nids sont uniquement tressés avec les végétaux qui

les soutiennent et non constitués de matériaux rapportés, par exemple en les soulevant délicatement pour trouver des feuilles encore vivantes rattachées à la plante support et dont l'extrémité effilochée est directement reliée à la construction.

Parallèlement aux recherches de nids, six localités ont été échantillonnées par piégeage non vulnérant, soit parce qu'elles présentaient un milieu optimum pour le Rat de moissons, mais sans présence de nid, soit parce qu'il s'avérait intéressant de se faire une idée de la taille d'une population. Aussi, comme ce petit rongeur évolue principalement à bonne hauteur dans les hautes herbes et qu'en conséquence le piégeage classique au sol n'est pas efficace (Vogel & Gander, 2015), il a fallu disposer des pièges sur des piquets à environ 60 cm du sol (Fig. 3). En outre, trois à quatre semaines de pré-nourrissage à l'aide



Fig. 2. Friche humide à Molinie (*Molinia arundinacea*), partiellement colonisée par des Roseaux (*Phragmites australis*) et des Solidages (*Solidago canadensis*), située au nord de l'ancien marais de Greny (commune de Péron - Ain), lieu même où ont été capturés 10 Rats des moissons en novembre 2016 (station 5).

de graines de tournesol décortiquées ont été nécessaires avant d'effectuer les premières sessions de capture.

Les piégeages ont été réalisés avec des pièges en bois de facture artisanale (Fig. 3) offrant une bonne protection thermique et conçus pour capturer des animaux de moins de 8 g. Disposés en ligne à trois ou quatre mètres l'un de l'autre dans les secteurs les plus favorables, ils permettent ainsi d'atteindre en automne, lors du pic démographique des micromammifères, un taux de réussite sur 12 heures souvent supérieur à 50% (toutes espèces confondues), pour autant qu'il y ait eu un pré-nourrissage.

RÉSULTATS

Résultats globaux

Contre toute attente, pas moins de 141 nouvelles données ont été récoltées attestant l'existence de Rats des moissons dans 12 nouveaux sites du bassin genevois (Fig. 1). Toutefois, aucune preuve de présence n'a été détectée ailleurs que dans le Pays de Gex (Ain) et le marais du Grand Bataillard (Vaud), ce dernier déjà connu depuis 1966 pour abriter l'espèce. Néanmoins, des recherches de nids

effectuées en 2015 dans ce site protégé ont permis la découverte de nouveaux secteurs de présence de l'espèce, notamment au sud du Grand Bataillard, sur la commune de Commugny, dans de petites magnocariçaises relativement isolées au bord de la Versoix (Gilliéron, 2015). En ce qui concerne la partie vaudoise du bassin genevois, notons que des prospections effectuées en 2016 au marais des Bœufs, le long de l'Asse et sur les marais de la Topaz (commune de Chésereux) se sont révélées négatives malgré la présence de quelques milieux relativement propices au Rat des moissons.

Pour ce qui est du canton de Genève, tout porte à croire que l'espèce n'y est pas ou plus présente. En effet, entre 2014 et 2016 une quinzaine de sites présentant des formations végétales relativement favorables au Rat des moissons ont été prospectés, mais sans succès. D'autre part, suite à la découverte en novembre 2016 de deux nids situés sur France à trois mètres environ de la frontière suisse et non loin du Mandement (donnée GPS confirmée par une borne), sur la commune de Thoiry (station 8; Fig. 4), toute la région frontalière proche située entre Malval et Bourdigny-Dessus a été méticuleusement prospectée durant deux jours, mais sans résultat



Fig. 3. Dispositif de piégeage utilisé pour la capture des Rats des moissons.

et sans découverte de milieux favorables à l'espèce, sauf vers Moulin Fabry où subsiste une petite zone humide colonisée essentiellement par des roseaux. Notons, par ailleurs, qu'en octobre 2007, six sites censés favorables à l'espèce avaient déjà été prospectés dans le canton de Genève et qu'aucun indice de présence n'y avait été découvert (Blant *et al.*, 2012).

En ce qui concerne la partie du bassin genevois située en Haute-Savoie, malgré de fortes présomptions de présence de l'espèce dans divers sites, aucun indice n'a été trouvé (Fig. 1). Parmi ces sites, les marais de Chilly et ceux de Marival, tous deux situés sur la commune de Loisin, ont fait l'objet en 2015 et 2016 de recherches systématiques de nids et de campagnes de piégeage sur plusieurs jours.

Résultats pour le Pays de Gex

Les nouvelles stations de présence de Rat des moissons du bassin genevois ont toutes été trouvées dans le Pays de Gex, entre les marais de l'Etournel (commune de Colonges) et le marais de Prodon (Fig. 5) situé au bord de la Versoix (communes de Grilly et Divonne-les-Bains), à des altitudes s'échelonnant de 328 à 520 m (Fig. 1;

Tab. 1). Les indices d'occupation ont été obtenus grâce à la découverte de 80 nids dans l'ensemble des sites (Tab. 2) et la capture de 61 individus dans trois stations.

DISCUSSION

Dans le bassin genevois, il ressort que le Rat des moissons est à ce jour absent du canton de Genève et de la Haute-Savoie. Toutefois, cette constatation ne permet pas d'affirmer que l'espèce n'y fut pas présente autrefois, notamment dans les anciens marais de la Seymaz (Choulex et Meinier, canton de Genève) et dans plusieurs sites du Bas-Chablais haut-savoyard où de très nombreux marais existaient encore jusque vers le milieu du XX^e siècle. D'autre part, il n'est pas impossible qu'une petite population résiduelle ait encore subsisté jusque vers le début des années soixante dans l'anse du Rhône située sous le Lignon (Vernier, canton de Genève), à l'emplacement de l'actuelle station d'épuration d'Aïre, là même où Schauenberg aurait trouvé en 1945 des nids et où se trouvait une zone marécageuse d'environ 3 ha (cf. introduction).



Fig. 4. Emplacement d'un nid de Rat des moissons trouvé en novembre 2016 (station 8), à trois mètres de la frontière suisse sur la commune de Thoiry (Ain), dans une lisière herbacée constituée en grande partie par des laïches (*Carex* sp.) et par quelques Roseaux (*Phragmites australis*).

Contrairement au Grand Bataillard, relativement épargné, tous les sites découverts se situent à l'emplacement d'anciens marais ou de zones prairiales qui jusque vers la fin du XIX^e siècle couvraient d'importantes surfaces, à l'exemple du complexe des anciens marais d'Arbère, de Prodon et de Divonne, dont la surface vers 1950 était encore proche de 200 ha. Aussi paraît-il vraisemblable que la plupart des stations découvertes constituent des zones de repli, sans véritable connexion apparente entre elles et où les populations résiduelles de Rats des moissons trouvent néanmoins des milieux de substitution sub-optimum, souvent fortement dégradés et menacés à très court terme par l'aménagement du territoire, l'urbanisation, l'agriculture intensive, le réseau routier ou par l'envahissement des néophytes. C'est notamment le cas d'une petite population située sur la commune de Saint-Jean-de-Gonville et à quelques encablures de la frontière suisse. A cet endroit, les Rats des moissons ne survivent en effet que grâce à la présence de bandes herbacées situées le long de la semi-autoroute qui relie Collonges à Saint-Genis-Pouilly et de fossés de drainage en plein

champs colonisés par des Roseaux (*Phragmites australis*) et des Solidages (*Solidago canadensis*), ainsi que par quelques laïches (*Carex* sp.) et quelques Faux roseaux (*Phalaris arundinacea*). A noter enfin qu'aucun indice de présence de Rat des moissons n'a été détecté au marais de Brou de même qu'au marais des Bidonnes (commune de Divonne-les-Bains), malgré la présence de quelques zones favorables, notamment d'une très belle magnocariçaie d'un demi hectare située au nord-est des étangs de Crassy.

L'absence actuelle d'une population de Rats des moissons dans la région du Mandement limitrophe avec le Pays de Gex (rive droite du canton de Genève) pourrait être liée à l'inexistence historique d'anciens bas-marais ou de sols pouvant favoriser la formation d'une haute végétation herbacée hygrophile propice à la présence de l'espèce. D'autre part, cette région présente de nombreux secteurs où les grands vignobles et les zones forestières interdisent toute progression d'une population française vers d'éventuels milieux favorables, notamment dans certaines zones de l'Allondon. Comme l'ont déjà fait



Fig. 5. Le marais de Prodon (station 12), situé sur les communes de Grilly et Divonne-les-Bains (Ain), jouxte sur la rive française de la Versoix celui du Grand Bataillard. Il présente encore quelques magnocariçaies favorables à la présence du Rat des moissons.

remarquer certains auteurs, la connectivité des habitats est en effet un facteur important pour nombre de micro-mammifères et sans doute encore plus pour le Rat des moissons qui ne peut se passer de haute végétation herbacée, du moins durant les trois quart de l'année (Darinet & Favier, 2014; Blant *et al.*, 2012; Wijnhoven *et al.*, 2006). Dans le Pays de Gex, le maintien de certaines populations ne dépend d'ailleurs que de la présence de corridors végétalisés, comme des canaux de drainage en plein champs, des ourlets en lisière humide (Fig. 4), des bandes herbeuses sur sol hygromorphe et même de certains tronçons de voie ferrée à l'abandon, qui sont autant de milieux, certes précaires, mais qui n'existent pas dans le Mandement genevois tout proche. Notons, par ailleurs, que les nids découverts dans le bassin genevois étaient pour l'essentiel construits dans des formations plus ou moins pures de grandes laïches, généralement *Carex acutiformis*, ce qui explique en partie l'intérêt du Rat des moissons pour les magnocariçaies qui constituent son habitat optimum (Tab. 2). Cet intérêt de l'espèce pour ce type de milieu a d'ailleurs très bien été démontré en 2015 lors d'une campagne de recensement de nids dans le marais du Grand Bataillard où 80% d'entre eux se trou-

vaient dans des groupements à *Carex acutiformis*, avec ou sans présence de *Phalaris arundinacea* (Blant, 2015). En ce qui concerne le Bas-Chablais haut-savoyard, l'absence du Rat des moissons, du moins présumée, est en revanche plus difficile à expliquer. Les anciennes cartes topographiques datant du milieu du XX^e siècle montrent en effet qu'il existait de nombreux bas-marais susceptibles d'abriter des populations plus ou moins importantes. D'ailleurs, certaines de ces zones humides subsistent encore, bien que fortement envahies par des ligneux et des néophytes, et présentent ici et là des milieux apparemment tout aussi favorables au Rat des moissons que ceux découverts dans le Pays de Gex. Tous ces bas-marais ont bien entendu été prospectés dans le cadre de cette étude, mais sans résultat. Comme il l'a été dit, les marais de Chilly et ceux de Marival (commune de Loisin) ont en outre fait l'objet de campagnes de captures précédées de quatre semaines de pré-nourrissage. Il en va de même pour les marais de Machilly et de Bons-en-Chablais (marais de la Dame et marais de Fully) qui également n'ont donné aucun résultat. Pour ce qui est des marais de Marival, qui présentent d'importantes prairies humides et sans doute les plus belles magnocariçaies du Bas-Cha-

Table 1. Localisation géographique des stations de présence de Rat des moissons nouvellement découvertes dans le bassin genevois et types d'indices de présence par date. Les numéros de station (gauche) correspondent à ceux géoréférencés à la figure 1.

	Localité, commune, altitude	Type d'habitat (description sommaire)	Captures (nb)	Nids (nb)	Date
1 a	L'Etournel, Collonges, 330 m	Magnocariçaie		10	16.08.2014
1 b	L'Etournel, Collonges, 328 m	Phalaridaie		1	16.08.2014
2	Baraty, Péron, 458 m	Lisière herbacée et cariçaie		3	30.10.2016
3	Entrée est de Péron, Péron, 520 m	Bande herbacée (800 m)		2	30.10.2016
4 a	Ancien marais de Greny sud, Péron, 470 m	Magnocariçaie		3	19.10.2016
4 b	Ancien marais de Greny sud, Péron, 470 m	Magnocariçaie		5	24.10.2016
4 c	Ancien marais de Greny sud, Péron, 470 m	Magnocariçaie	7		04.11.2016
5 a	Ancien marais de Greny nord, Péron, 460 m	Moliniaie et phragmitaie		2	19.10.2016
5 b	Ancien marais de Greny nord, Péron, 460 m	Moliniaie et phragmitaie	10		04.11.2016
6 a	La Biole, Saint-Jean-de-Gonville, 460 m	Bande herbacée et roseaux		8	04.11.2016
6 b	La Biole, Saint-Jean-de-Gonville, 460 m	Banquette herbacée		1	23.11.2016
6 c	La Biole, Saint-Jean-de-Gonville, 460 m	Ruisselet végétalisé		1	28.10.2016
6 d	La Biole, Saint-Jean-de-Gonville, 460 m	Friche humide avec <i>Carex</i> sp.		2	28.10.2016
7	Le Grand Marais, Fénière, 464 m	Magnocariçaie		1	23.11.2016
8	Chante-Merle, Thoiry, 440 m	Lisière herbacée		2	23.11.2016
9	Bois du Grand Journans, Chevry, 465 m	Magnocariçaie en lisière		3	29.10.2016
10 a	Bief de Janvain, Chevry, 466 m	Prairie et magnocariçaie		9	29.10.2016
10 b	Bief de Janvain, Chevry, 466 m	Magnocariçaie riveraine		2	23.11.2016
11	La Praslée, Chevry, 505 m	Fossé végétalisé et prairie		10	29.10.2016
12 a	Marais de Prodon, Divonne-les-Bains, 466 m	Magnocariçaie	1		02.06.2015
12 b	Marais de Prodon, Divonne-les-Bains, 466 m	Magnocariçaie		1	11.08.2015
12 c	Marais de Prodon, Divonne-les-Bains, 466 m	Magnocariçaie	17		12.08.2015
12 d	Marais de Prodon, Divonne-les-Bains, 466 m	Magnocariçaie		2	30.08.2016
12 e	Marais de Prodon, Divonne-les-Bains, 466 m	Magnocariçaie		8	21.07.2015
12 f	Marais de Prodon, Divonne-les-Bains, 466 m	Magnocariçaie	15		30.08.2016
12 g	Marais de Prodon, Divonne-les-Bains, 466 m	Magnocariçaie	1		31.08.2016
12 h	Marais de Prodon, Divonne-les-Bains, 466 m	Magnocariçaie	10		14.09.2016
12 i	Marais de Prodon, Grilly, 465 m	Magnocariçaie		2	21.07.2015
12 j	Marais de Prodon, Grilly, 465 m	Magnocariçaie		2	11.08.2015

blais, son isolement dans un cadre forestier pourrait être la cause de l'absence d'une population résiduelle de Rats des Moissons. Cependant, l'absence d'indices de présence dans la partie haut-savoyarde du bassin genevois ne signifie pas pour autant qu'il n'y existe pas ou plus de populations de Rats des moissons. Plusieurs sites de moindre importance, en effet, mériteraient d'être prospectés, car, tel qu'on a pu le constater dans le Pays de Gex mais aussi dans d'autres régions d'Europe comme en Carinthie (Komposch, 2002), ce rongeur peut passer totalement inaperçu durant des décennies si des recherches ciblées ne sont pas entreprises. Il n'est donc pas interdit de penser qu'il existe peut-être dans le Bas-Chablais haut-savoyard des populations survivantes retranchées dans des milieux secondaires.

CONCLUSION

Malgré la découverte de douze nouvelles petites populations de Rats des moissons dans le bassin genevois, alors que jusqu'en 2014 on ne connaissait qu'un seul site de présence confirmé, rien ne permet d'avancer que l'espèce n'est pas menacée à l'échelle de cette région. En effet, aucun des sites occupés par ce petit rongeur ne bénéficie d'une quelconque protection, à l'exception des marais de Fénière et de l'Etournel, dotés d'un arrêté de biotope, et de celui du Grand Bataillard, qui constitue une réserve de faune répertoriée dans la liste suisse des bas-marais d'importance nationale et qui dispose à ce titre d'une maîtrise foncière de conservation adaptée à la sauvegarde de l'espèce. D'autre part, il est important de souligner que presque toutes les populations du Pays de Gex consti-

Table 2. Nids de Rat des moissons trouvés dans le Pays de Gex classés par station et par catégorie de végétaux principaux qui ont servi à leur confection. La colonne de gauche renvoie aux numéros de stations figurant sur la Figure 1.

Station	Localité, commune	Carex acutiformis ou Carex spp. (> 0,80 cm)	Phalaris arundinacea	Molinia arundinacea	Poacées diverses (> 0,80 cm)	Total
1	L'Etournel, Collonges	10	1			11
2	Baraty, Péron	1			2	3
3	Entrée est de Péron, Péron	1		1		2
4	Ancien marais de Greny sud, Péron	8				8
5	Ancien marais de Greny nord, Péron			2		2
6	La Biole, Saint-Jean-de-Gonville	4	8			12
7	Le Grand marais, Fénière	1				1
8	Chante-Merle, Thoiry	2				2
9	Bois du Grand Journans, Chevry	3				3
10	Bief de Janvain, Chevry	11				11
11	La Praslée, Chevry			5	5	10
12	Marais de Prodon, Divonne-les Bains	15				15
		56	9	8	7	80

tuent de petits isolats menacés à court ou moyen terme de disparition si des mesures de protection ne sont pas engagées rapidement. Pour n'occuper parfois qu'un ou deux hectares de milieu favorable, certaines populations sont à ce point si petites qu'on peut être même étonné qu'elles puissent encore de nos jours survivre dans un environnement de plus en plus soumis à l'urbanisation et aux pratiques agricoles intensives. Les premières évaluations de menace (cf. Fig. 1) mériteraient cependant d'être affinées afin de déterminer les mesures de protection à prendre pour les rendre viables sur le long terme. Bien entendu, de telles mesures dépendent des choix politiques sur l'aménagement territorial et de la valeur patrimoniale qui est attribuée localement à la biodiversité. Enfin, soulignons que le Rat des moissons ne bénéficie en France d'aucune protection légale, alors qu'en Suisse l'espèce est non seulement protégée, mais aussi inscrite comme « espèce menacée » (catégorie 3) dans la Liste rouge de l'Office fédéral de l'environnement et du paysage (Duelli, 1994).

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Identification of the polyp stage of three leptomedusa species using DNA barcoding

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Abstract

DNA sequence data of hydromedusae and hydroids collected in the fjords near Bergen, Norway, permitted to connect three leptomedusae to three thecate hydroids with hitherto unknown life cycles. For all three species pairs, identical 16S and 18S sequences could be found. For comparisons, estimates of intraspecific variation of 16S sequences of other leptomedusa species were determined by comparing specimens collected at different localities. The sequence comparisons allowed us to conclude that *Ptychogena crocea* Kramp & Dumas, 1925 is the medusa stage of the hydroid *Stegopoma plicatile* (M. Sars, 1863), *Earleria quadrata* (Hosia & Pages, 2007) the medusa of *Racemoramus panicula* (G.O. Sars, 1874), and *Cyclocanna welshi* Bigelow, 1918 the medusa of *Egmundella producta* (G.O. Sars, 1874). Due to non-matching geographic distribution patterns of the medusa and hydroid phases, as well as the possibility that other related medusa species may have morphologically identical hydroids, the identities of *Stegopoma plicatile* and *Racemoramus panicula* are considered ambiguous. These nominal species likely refer to species complexes. Their names are therefore considered as partial synonyms of the medusa-based names and the latter should remain in use despite being more recent. *Cyclocanna welshi* and *Egmundella producta* are recognised as synonyms, and the species should from now on be referred to as *Cyclocanna producta* (G.O. Sars, 1874) n. comb.

Keywords: Cnidaria - Hydrozoa - Leptothecata - marine - hydromedusae - hydroids - life cycles.

INTRODUCTION

The life cycles of many hydromedusae and hydroids remain unknown because they are rare or difficult to cultivate. DNA barcodes, namely mitochondrial 16S and COI sequences, have recently emerged as a useful tool to unravel hydrozoan life cycles through matching sequences obtained from medusae and hydroids. Two recent papers have thus identified the polyp stage of *Oceania armata* Kölliker, 1853 (Schuchert, 2016b) and connected the polyp *Boreohydra simplex* Westblad, 1937 with the medusa *Plotocnide borealis* Wagner, 1885 (Pyataeva *et al.*, 2016).

During the last decade, the authors have sampled hydroids and medusae in Norway, mostly in the fjords near Bergen. The specimens were used for various taxonomic and systematic research, including DNA based phylogenetics and constructing barcode databases for the molecular identification of hydrozoans. A recent sampling in the deep waters of Korsfjord and Raunefjord

yielded three leptomedusa species whose 16S and 18S sequences matched those of polyp stages collected in the same region.

Here we present a synthesis of these results with a re-evaluation of the life cycle and taxonomy of the three Leptothecata species.

MATERIAL AND METHODS

Thecate hydroids were collected on various substrates by dredging. Leptomedusae were collected from various depths and locations using plankton nets of different sizes (details on the new material are given in Appendix 1). For depths below 70 m, a modified WP3 plankton net with a non-filtering cod-end and 750 µm mesh size was used. For species identification we used Kramp (1959), Cornelius (1995) and other works mentioned in the Taxonomy part.

DNA extracts and 16S sequences were obtained as

given in Schuchert (2005, 2016b). Most 18S sequences were determined as described in Leclère *et al.* (2009), except for three (marked with § in Appendix 1) which were retrieved by BlastN from transcriptome assemblies (L. Leclère, C. Dunn, and C. Munro, unpublished data). Alignments and phylogenetic analyses were performed as given in Schuchert (2005, 2016b). The aligned 16S sequences were trimmed to the position of the 3' ends of the primers SHA/SHB which were used for this study (Cunningham & Buss, 1993). The aligned 18S sequences were trimmed to the shortest available sequence. Differences between sequence pairs were quantified using p-distances (uncorrected base-pair differences in %, Collins *et al.*, 2012) using the software Bioedit (Hall, 1999).

In order to have a wider spectrum of species for comparisons, all suitable 16S sequences of leptomedusae (excluding Campanulariidae) found in the GenBank database were also included in the analyses (GenBank accession numbers can be taken from Figs 1-2). The Campanulariidae form a distinct, separate clade (Leclère *et al.*, 2009; Maronna *et al.*, 2016) and were excluded from our analysis as they do not contribute additional information. Additional sequencing of COI and 16S was carried out at the CCDB (<http://ccdb.ca/resources/>) for some medusa specimens, with the sequences deposited in the BOLD database (Appendix 2). As these 16S sequences represented the same haplotypes as given in Appendix 1, they were not included in the final analysis in order to avoid dense, unreadable phylogenetic trees.

Abbreviations

BOLD	The Barcode of Life Data System (see Ratnasingham & Hebert, 2007), http://boldsystems.org
CCDB	Canadian Centre for DNA Barcoding
GenBank	Genetic sequence database of the National Institute of Health, USA, http://www.ncbi.nlm.nih.gov/genbank
MHNG	Muséum d'histoire naturelle de Genève, Switzerland

RESULTS AND DISCUSSION

Maximum likelihood analyses

16S and 18S sequence data were used to obtain Maximum Likelihood trees (Figs 1-2) which graphically visualise inter- and intraspecific sequence divergences. Comparing the length of the branches separating the samples allows rapid identification of identical or highly similar sequences found for polyp and medusa stages (Figs 1-2, highlighted in red), as well as the visualisation of the intraspecific distances seen in a few other species (highlighted in blue).

The mitochondrial 16S gene sequence tends to be a reliable marker for Hydrozoa (Miglietta *et al.*, 2007,

2009, 2015; Schuchert, 2005, 2016b; Zhang *et al.*, 2015), but for species-level relationships it is advisable to include also a nuclear marker in order to exclude misleading effects of past introgressions or hybridisations on the mitochondrial markers (e. g. like in Miller *et al.*, 2012). We used the nuclear 18S gene sequence to complement the results obtained using the 16S data, as they were available from other studies for a good number of the species and samples used here. Although 18S is not an ideal barcoding marker due its relatively low interspecific variability, in the present data set the species were sufficiently well separated and the polyp-medusa matches were also seen in with the 18S sequences (Fig. 2, Table 2), thus adequately complementing the 16S results. Neither 16S nor 18S resolves satisfactorily the phylogenetic relationships at the family level. However, this was not the aim of this study and will be the subject of a forthcoming publication using more markers and taxa (L. Leclère, unpublished data).

16S and 18S intraspecific variation

The substitution rate of the mitochondrial 16S gene varies considerably within the Leptothecata subclades (Leclère *et al.*, 2009; compare also Cunha *et al.*, 2016 for COI). To quantify the extent of intraspecific variation within the leptomedusae, we calculated maximum p-distances for available pairs of conspecific specimens from different localities (Table 1). The observed values ranged from 0.34 to 1.18% and are lower than values observed for other hydrozoans [up to 4.4 % in Oceaniidae (Schuchert, 2016b); 5.5% in Corynidae (Schuchert, 2005); 19.6% in *Plumularia setacea* (Schuchert, 2014), but the Plumulariidae have a higher substitution rate (Leclère *et al.*, 2009) and *P. setacea* could be a species complex]. For the 18S sequence only four preliminary estimates for the intraspecific divergences could be obtained (Table 2). These values allow evaluating sequence divergences other than perfect matches between polyp and medusa samples (Table 3).

Ptychogena crocea and *Stegopoma plicatile*

16S sequences obtained from three *P. crocea* medusae (Fig. 3) and two samples of the hydroid *Stegopoma plicatile* (Fig. 4), all collected in the vicinity of Bergen (Appendix 1), were identical. Likewise, also 18S and COI sequences were identical (COI: GenBank JN109191, BOLD specimens HYPNO_314 & HYPNO_286). These results indicate that the hydroid identified as *Stegopoma plicatile* is the polyp stage of *P. crocea*. In the 16S tree, its congener *Ptychogena lactea* appeared as a sister-species, although well separated from *P. crocea*. Other members of the Laodiceida clade (Maronna *et al.*, 2016), such as *Modeeria rotunda*, clustered nearby. *Ptychogena crocea* is a distinct and conspicuous medusa

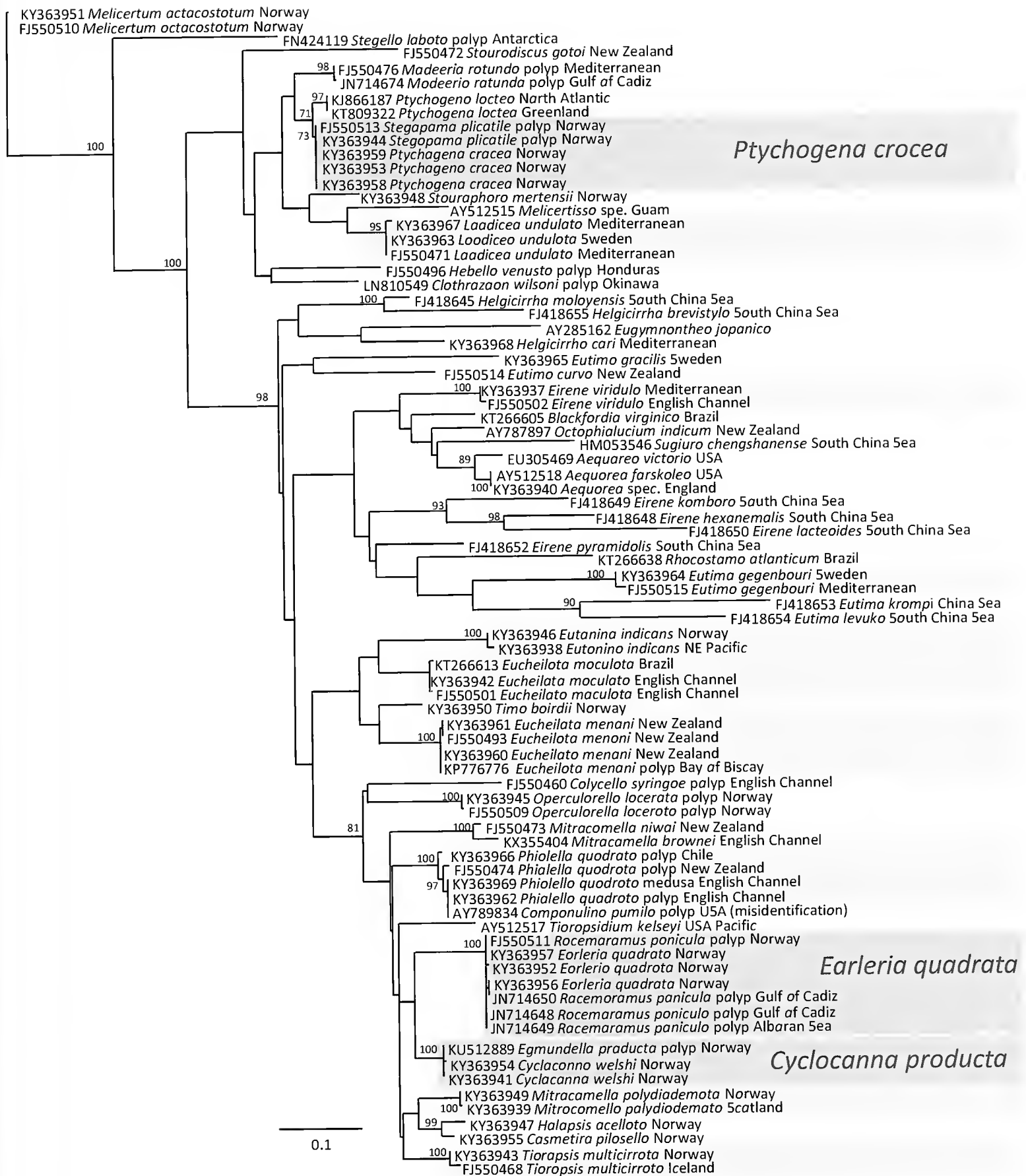


Fig. 1. 16S maximum likelihood phylogenetic tree of leptomedusan species obtained with PhyML (GTR+G+I model) and based on 605 bp positions of the mitochondrial 16S gene. Node-support values are bootstrap values of 100 pseudoreplicates (shown only if > 70%). For more details see text and Appendix 1.

Samples based on the polyp stage are indicated, all others are medusa samples. Highlighted in red are matching medusa and polyp stage samples. Highlighted in blue are samples used to estimate intraspecific variability (Table 1).

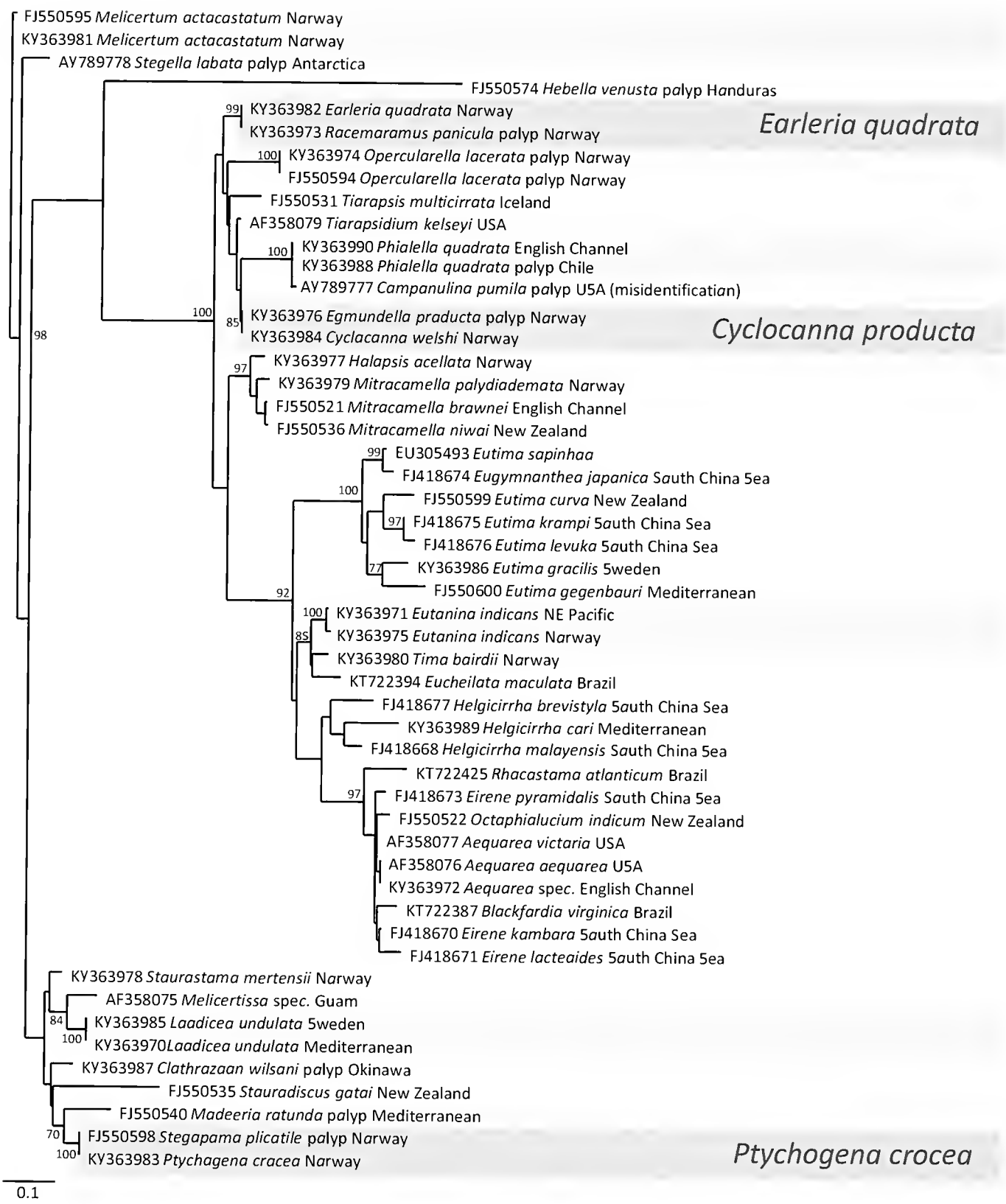


Fig. 2. 18S maximum likelihood phylogenetic tree of leptomedusan species obtained with PhyML (GTR+G+I model) and based on 1665 bp positions of the nuclear 18S gene. Node-support values are bootstrap values of 100 pseudoreplicates (shown only if > 70%). For more details see text and Appendix 1. Samples based on the polyp stage are indicated, all others are medusa samples. Highlighted in red are matching medusa and polyp stage samples. Highlighted in blue are samples used to estimate intraspecific variability (Table 2).

Table 1. Maximal observed intraspecific p-distance values (%) of 16S sequences of Leptothecata with a medusa stage.

species and localities	distance
<i>Eirene viridula</i> Villefranche KY363937 - English Channel FJ550502	0.51
<i>Eucheilota maculata</i> Brazil KT266613 - English Channel FJ550501	0.51
<i>Eucheilota menoni</i> New Zealand FJ550493 - Bay of Biscay KP776776	0.34
<i>Eutima gegenbauri</i> Mediterranean FJ550515 - Sweden KY363952	0.84
<i>Laodicea undulata</i> Sweden KY363963 - Mediterranean FJ550471	0.50
<i>Mitrocomella polydiademata</i> Norway KY363949 - Scotland KY363939	0.17
<i>Phialella quadrata</i> New Zealand FJ550474 - Chile KY363966	1.18
<i>Tiaropsis multicirrata</i> Iceland FJ550468 - Norway KY363943	0.84

Table 2. Selected examples of maximal observed intraspecific p-distance values (%) of the 18S marker.

species and localities	distance
<i>Eutonina indicans</i> Norway KY363975 - NE Pacific KY363971	0.24
<i>Laodicea undulata</i> Sweden KY363985 - Mediterranean KY363970	0
<i>Melicertum octocostatum</i> Norway, intrapopulation, KY363981 - FJ550595	0.12
<i>Phialella quadrata</i> English Channel KY363990 - Chile KY363966	0

Table 3. Observed minimal and maximal p-distances in %, for details of the used species and samples see Appendix 1.

species or species pairs	16S	18S
within <i>Ptychogena crocea</i> (KY363953, KY363959, KY363958)	0	one sample
within <i>Stegopoma plicatile</i> (FJ550513, KY363944)	0	one sample
<i>Ptychogena crocea</i> - <i>Stegopoma plicatile</i>	0	0
within <i>Earleria quadrata</i> (KY363952, KY363957, KY363956)	0.17 - 0.34	one sample
within <i>Racemoramus panicula</i> (JN714650, FJ550511, JN714649, JN714648)	0 - 0.39	one sample
<i>Earleria quadrata</i> - <i>Racemoramus panicula</i>	0 - 0.17	0
within <i>Cyclocanna welshi</i> (KY363954, KY363941)	0.17	one sample
within <i>Egmundella producta</i> KU512889	one sample	one sample
<i>Cyclocanna welshi</i> - <i>Egmundella producta</i>	0 - 0.17	0

and easily identifiable. Its intensively orange-yellow manubrium and gonad pouches makes it very visible in plankton samples, even young stages (Fig. 3D). In addition to its yellow-orange colour, the characteristic lateral perradial stomach diverticula (gonad pouches, Fig. 3B) are very large and not attached to the subumbrella. Preserved material can nevertheless be confused with *Modeeria rotunda* (Quoy & Gaimard, 1827) and *Chromatonema rubrum* Fewkes, 1882, which also occur in deep waters of the North Atlantic (see Kramp, 1919, 1920, 1959; Russell, 1953; Edwards, 1973; Bleeker & van der Spoel, 1988; Cornelius, 1995; Schuchert, 2001; Pagès *et al.*, 2006).

Modeeria rotunda has a reddish-brown manubrium and characteristic interr radial subumbrellar pockets giving the impression that the manubrium is partly sunken into the mesogloea. *Chromatonema rubrum* has relatively small, white lateral gonad pouches and an orange to brown-reddish manubrium (Kramp, 1919, 1920). In addition, the cnidomes of the species differ: while *P. crocea* has 14-15 µm long microbasic mastigophores, *C. rubrum* and *Modeeria rotunda* have microbasic euryteles (19-20 µm and 25 µm; Russell, 1940). The congener *Ptychogena lactea* A. Agassiz, 1865, which also occurs in the NE Atlantic, has gonads on thinner

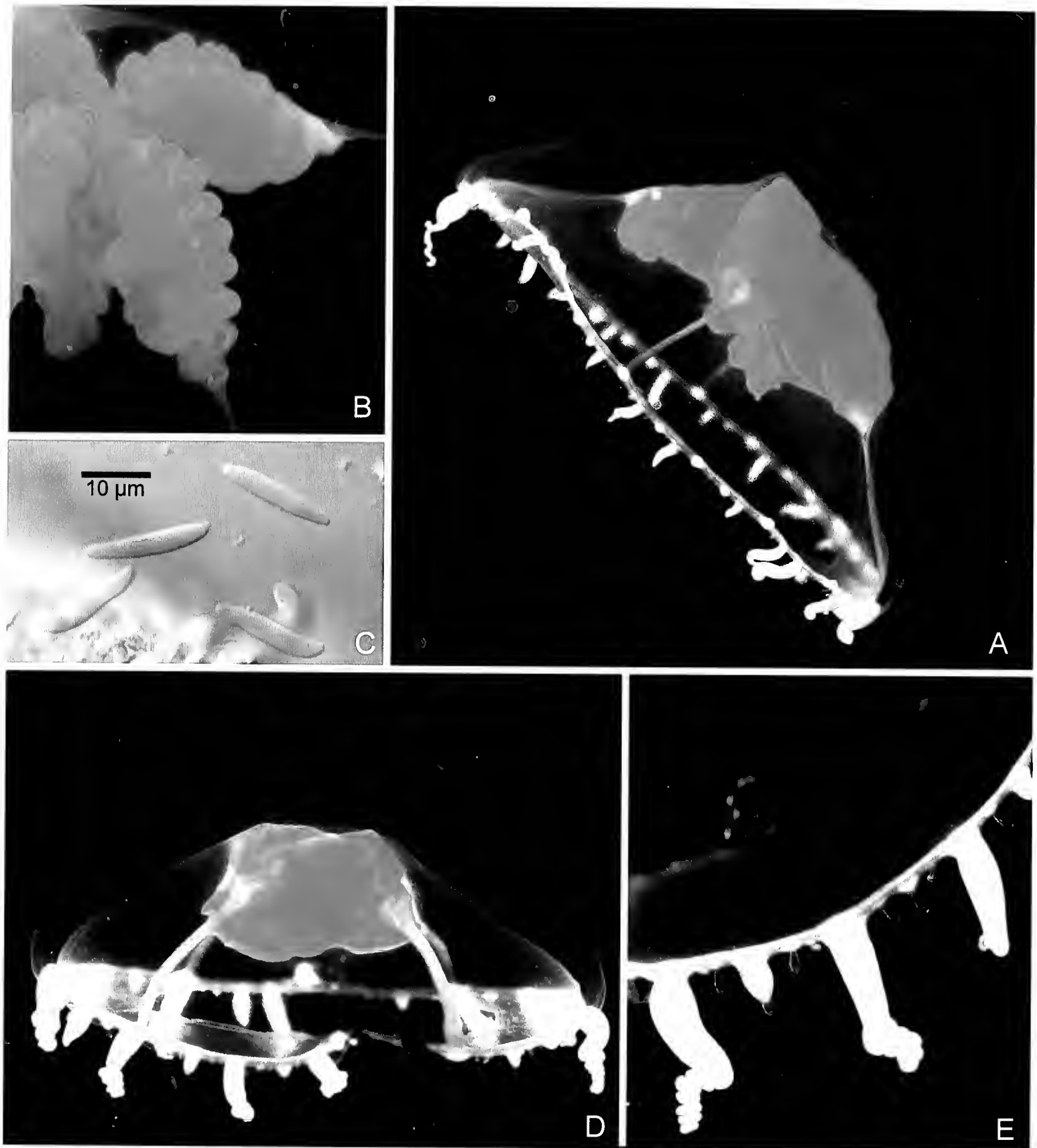
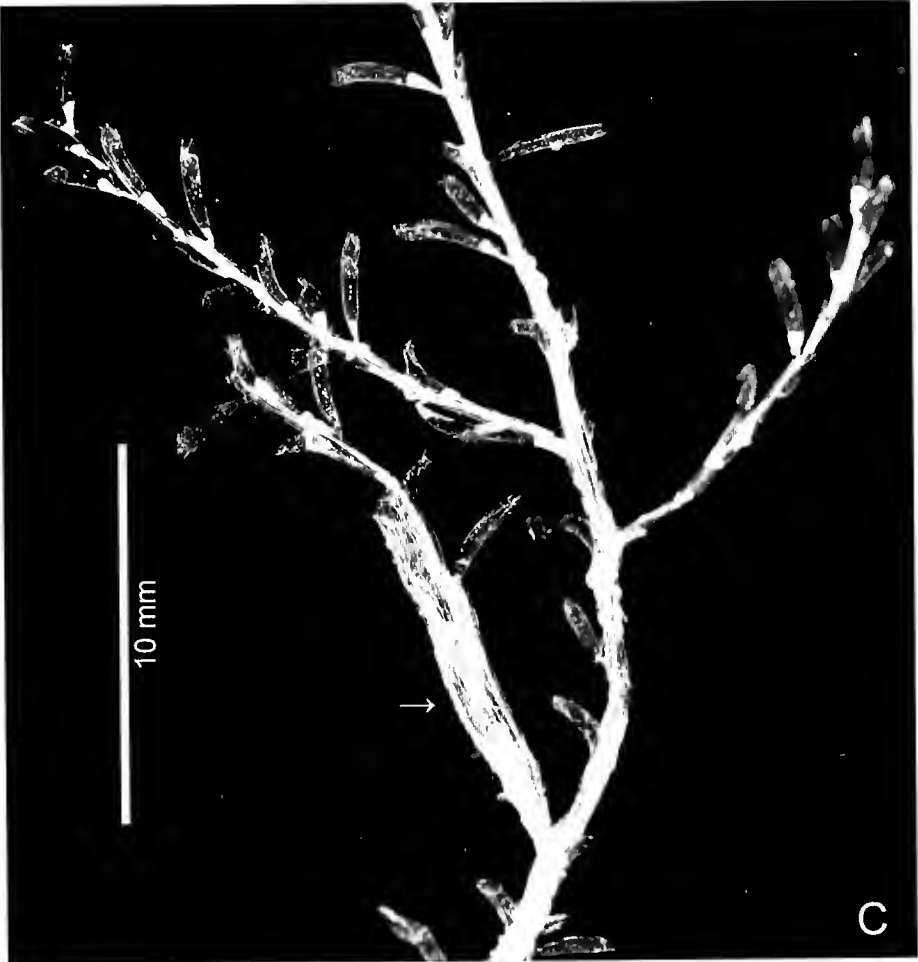
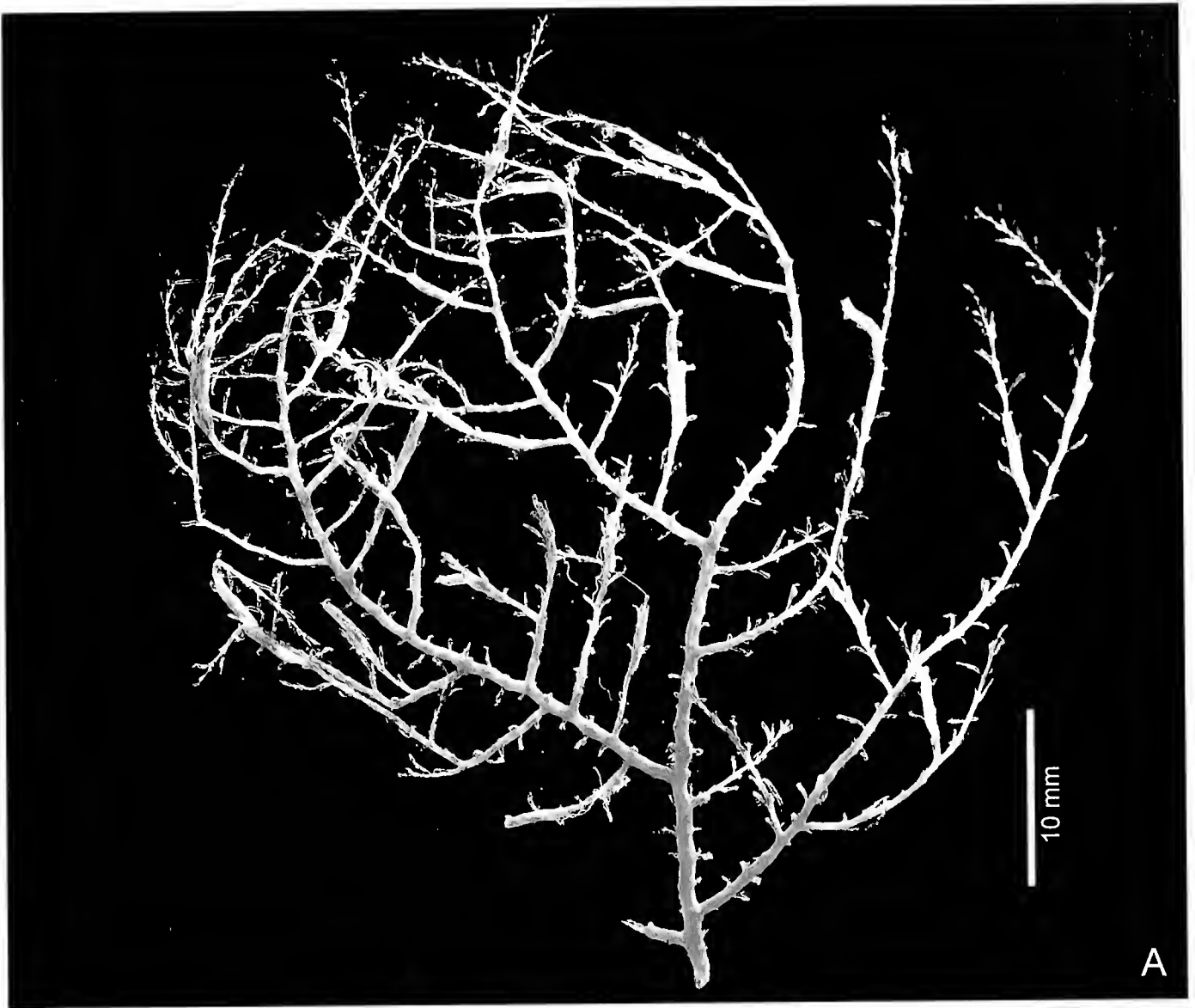


Fig. 3. *Ptychogena crocea* Kramp & Dumas, 1925, living medusae, except C, from Korsfjord, Norway. (A) MHNG-INVE-94101, lateral view, bell diameter 23 mm height 14 mm. (B) Same specimen as in A, close up of gonads. (C) Same specimen as in A, nematocysts. (D) Younger individual, used to obtain DNA isolate 1163. (E) Same as D, close up of bell margin seen from oral side, showing tentacles, tentacle stumps and several cordyli.

Fig. 4. *Stegopoma plicatile* (M. Sars, 1863), preserved sample MHNG-INVE-69614 (yielding DNA isolate 803) from Korsfjord, Norway, 650 m. (A) Whole colony. (B) Hydrotheca. (C) Branch with gonotheca (arrow). ►



and more numerous lateral diverticula that are attached to the subumbrella. Their colour differs also from *P. crocea*, being white, or with a peachy or greenish tint. More details and illustrations of these two *Ptychogena* species will be presented in a forthcoming publication (P. Schuchert, unpublished data).

Ptychogena crocea is a deep-water medusa with a rather restricted distribution and has so far been reported mostly along the Norwegian coast (Kramp & Dumas, 1925; Kramp, 1933, 1961; Rees, 1952; Hosia & Båmstedt, 2007), but there are also records of single specimens from the Cape Verde Islands and from the Gulf of Maine (Léon *et al.*, 2007). However, these two records need to be confirmed by new samples as at least the one from the Cape Verde had an atypical colour and could have been *Chromatonema rubrum*.

In contrast, the hydroid *Stegopoma plicatile* has a very wide, circumglobal distribution (Vervoort, 1972; Edwards, 1973; Cornelius, 1995; Calder, 2012). It is widespread in the Arctic and reaches as far south as Sweden and into deep waters off Brittany. It has also been reported in Boreal and Arctic regions of the Pacific and scattered points in the Southern Hemisphere and Antarctica. The type material came from Norway. Although the species has been described repeatedly, the reproduction of *S. plicatile* remained unknown for a long time until Schuchert (2001) reported for the first time that it releases a medusa. This was also observed for one of the current samples (MHNG-INVE-69614) which produced medusae of about 2 mm in diameter with four perradial tentacles, small interrational bulbs and 1–3 cordyli per quadrant. There were no ocelli or statocysts present. The stomach was distinctly cruciform in cross-section and lacked the yellow colour. Unfortunately, it was not possible to cultivate the medusae for more than two days.

We can conclude from our sequence analyses that the hydroid from the vicinity of Bergen identified as *Stegopoma plicatile* is the polyp stage of *Ptychogena crocea*. The taxonomic consequences, however, are more difficult to assess. The markedly different distribution patterns of the endemic, medusa-based species *Ptychogena crocea* and the widely distributed polyp-based *Stegopoma plicatile* strongly suggest that the latter is most probably a complex of cryptic species. The morphology of the *Stegopoma* hydroids is rather simple and poor in diagnostic features (see Cornelius 1995; Schuchert, 2001), and it is likely that other medusae related to *Ptychogena crocea* might have nearly identical hydroids. Several Leptothecata are known to have indistinguishable or very similar hydroid stages, but distinct medusae [e. g. “*Cuspidella*”-type hydroids producing medusae of the genera *Cosmetira* Forbes, 1848 or *Mitrocomella* Haeckel, 1879, “*Campanulina*”-type hydroids giving rise to medusae of the genera *Eucheilota* McCrady, 1859 and *Eutonina* Hartlaub, 1897 (Cornelius, 1995)].

The related medusa *Modeeria rotunda* has polyps with hydrothecae identical to those of *Stegopoma plicatile*, but with a colony that remains stolonial according to our current knowledge (Edwards, 1973; Cornelius, 1995; Schuchert, 2001). In the northern Atlantic Ocean, there are two further related medusa species with unknown polyp stages that potentially have a *Stegopoma*-like polyp stage: *Ptychogena lactea* and *Chromatonema rubrum*. Naumov (1969) attributed a “*Cuspidella*”-like hydroid (Bouillon *et al.*, 2006) to *Ptychogena lactea* because he found them to have a similar distribution in the Arctic Sea. This is, however, not a convincing argument and the polyp of *P. lactea* must be considered unknown. *Ptychogena lactea* is primarily an Arctic species and the distribution of *Stegopoma plicatile* (Schuchert, 2001) also matches its occurrence. The morphologically similar *Chromatonema rubrum* is a rare oceanic medusa, but has a much wider distribution (Kramp, 1919, 1959; Bleeker & van der Spoel, 1988). It occurs in deep waters (406–1750 m; Bleeker & van der Spoel, 1988). To our knowledge, the medusa has not been found in coastal waters of Norway, but only far off the continent (Kramp, 1919; Fraser, 1974; Bleeker & van der Spoel, 1988; Licandro *et al.*, 2015). Even if the discussed two medusae do not occur in coastal waters of Norway, they remain candidates for having a *Stegopoma*-like hydroid. So do the other *Ptychogena* medusae known from outside the region of the NE Atlantic: *P. antarctica* Browne, 1907, *P. californica* Torrey, 1909, and *P. hyperborea* Kramp, 1942.

When describing *Stegopoma plicatile*, Sars (1863) had material from four localities reaching from near Bergen, through Tromsø, to the northern tip of Norway in the Barents Sea. To our knowledge, no lectotype has been selected, and thus a more precise type locality cannot be given. *Stegopoma plicatile* was also designated by Totton (1930) as the type species of the genus.

While it is clear that *Ptychogena crocea* medusae are produced by hydroids referable to *Stegopoma plicatile*, it is still possible that even the type material of the latter was composed of several species. We therefore refrain from fully synonymising the two names and applying the senior name *Stegopoma plicatile* to the medusa *Ptychogena crocea* or suggesting a new combination of the two names. Synonymising the two names would lead to a confusing situation in which an endemic medusa has the name of a circumglobally distributed hydroid and which is likely a species complex. In the synonymy given below, *Stegopoma plicatile* is thus taxonomically only considered as a partial synonym. A similar situation was found for the medusa treated in the following.

Earleria quadrata* and *Racemoramus panicula

Earleria quadrata medusae (Fig. 5, GenBank number KY363957) and a *Racemoramus panicula* hydroid

(GenBank FJ550511) from the same region proved to have identical 16S (Fig. 1) and 18S sequences (Fig. 2; KY363982, KY363973¹). Several medusae of *Earleria quadrata* could be examined and they showed low 16S sequence variation of up to 2 bp differences per about 590 bp total length (Fig. 1, Table 3). This is compatible with intraspecific variation observed in other leptomedusan species (Table 1). Interestingly, three 16S sequences derived from *Racemoramus panicula* from the Gulf of Cadiz and the Alboran Sea (identified by C. Moura, JN714648 through JN714650) were very similar to the Norwegian samples, one of them (JN714648) even identical to both the medusa *Earleria quadrata* (KY363957) and the hydroid derived sequence (FJ550511). *Earleria quadrata* is unmistakable among Norwegian leptomedusae due to its intensively deep-purple pigmented manubrium with white lips (Fig. 5). The numerous open statocysts (1-3 between each of the up to 40 tentacles) with 6 or more concretions in a single row are also rather characteristic. *Earleria quadrata* is endemic to the coastal waters of Norway and the genus currently comprises six species (Schuchert, 2017). The polyp stage was hitherto only known for the Californian *Earleria corachloae* Widmer, Cailliet & Geller, 2010.

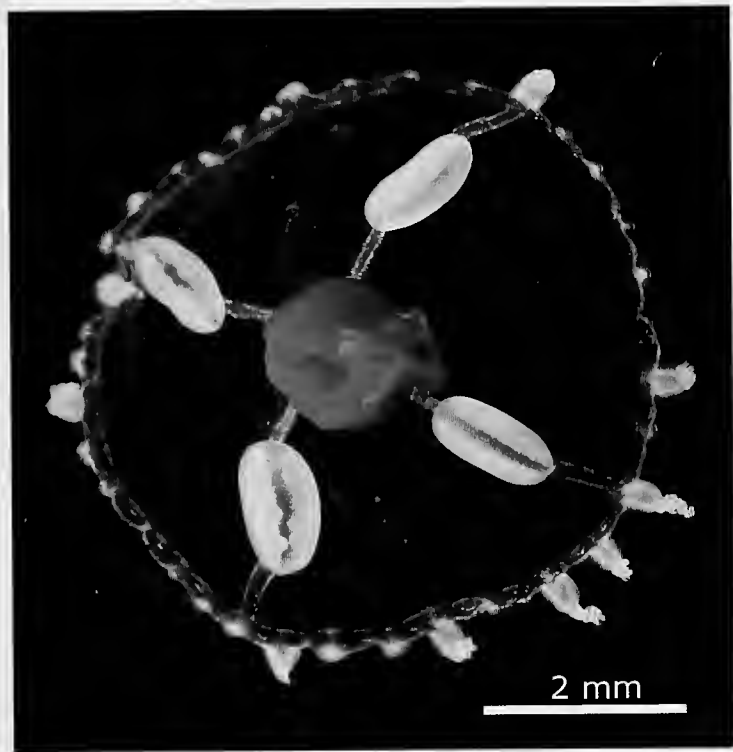


Fig. 5. *Earleria quadrata* (Hosia & Pages, 2007), living medusa from Korsfjord, one individual in a catch of four used to obtain DNA isolate 1162.

1 Resequencing the sample of *R. panicula* used to obtain the 18S sequence FJ550596 showed that it had two possible sequencing errors. Because the new sequence is also longer and the genus name has meanwhile changed, a new GenBank submission was made (KY363973).

While *Earleria quadrata* is only known very locally from deep waters of the Korsfjord south of Bergen (Hosia & Pages, 2007), the hydroid *Racemoramus panicula* has a very wide distribution. It occurs circumglobally in temperate to tropical regions, at depths of 20-5200 m (Schuchert, 2001; Calder, 2012). This extensive range made Calder (2012) doubt whether the observations represent a single species, prompting him to exclude records from the Pacific Ocean and attribute them to *R. denticulata* (Clarke, 1907), a species which so far had often been regarded as conspecific with *R. panicula*. The type locality of *R. panicula* is the Oslofjord (Norway) in a depth of 91-110 m (G. Sars, 1874). Among the Campanulinidae, *Racemoramus* has a quite unique colony structure, consisting of an unbranched stem from which groups of “*Campanulina*”-like hydrothecae originate at intervals (Fig. 6 and Cornelius, 1995; Schuchert, 2001; Calder, 2012). Calder (2012) therefore proposed to keep it distinct from the genera *Campanulina* van Beneden, 1847 and *Opercularella* Hincks, 1868. No life cycle of any *Racemoramus* species is known so far, although Rees & Rowe (1969) found that *Racemoramus panicula* from Sweden releases a medusa. *Earleria corachloae*, the only hitherto known hydroid of the genus *Earleria*, has branched colonies

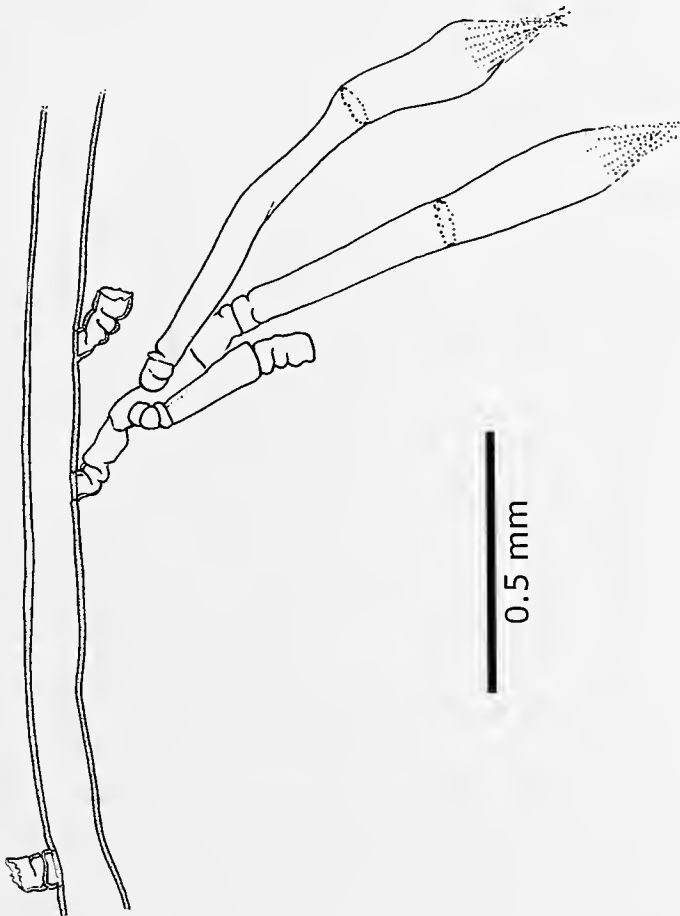


Fig. 6. *Racemoramus panicula* (G. O. Sars, 1874), sample MHNG-INVE-48748 from Korsfjord after DNA extraction, schematic drawing of part of main stem and some side-branches (some broken off).

that correspond with the traditional diagnosis of the genus *Campanulina* van Beneden, 1847 as proposed by Bouillon *et al.* (2006).

While it is very probable that Sars' material of *Racemoramus panicula* is the polyp stage of *Earleria quadrata* and the latter is thus a junior synonym, the hydroid *Racemoramus panicula* as used today – even in the restricted sense of Calder (2012) – is most likely a species complex. The disparate distributions of the medusa and the hydroid stage support this hypothesis. Therefore, we prefer to conclude more precisely that the medusa of *Earleria quadrata* has a polyp stage that corresponds to the morphology of *Racemoramus panicula*, but that both names are better not fully synonymised until a world-wide molecular genetic study of *Racemoramus* permits delimiting the different populations and their distributions. We should thus continue to use the name of the medusa for this species for the time being.

As mentioned above, polyps of *Racemoramus panicula* from the Gulf of Cadiz and the Mediterranean had 16S sequences which were identical or very similar to the Norwegian medusa *E. quadrata*. This extends the likely distributional range of this medusa close to that of the morphologically similar Mediterranean medusa *Earleria antoniae* (Gili *et al.*, 1998). It is therefore advisable to molecularly assess the species status of these two *Earleria* species to exclude the possibility of them representing morphologically divergent populations of the same species.

The taxonomic consequences at the family level are discussed in the next section.

Cyclocanna welshi and *Egmundella producta*

The two available samples of the medusa *Cyclocanna welshi* yielded 16S haplotypes differing only in one bp position. One of them was identical to the 16S obtained from the sample of *Egmundella producta* polyp described and figured by Schuchert (2016a). Likewise, the two 18S sequences were identical for polyp and medusa.

Cyclocanna welshi is a highly distinctive medusa. Its four radial canals and the gonads along them make a sharp bend shortly before reaching the circular canal and continue running along the circular canal before giving into it, resulting in a pattern reminiscent of a swastika (Fig. 7). Moreover, there are two types of tentacles: four large perradial tentacles with large bulbs situated at the marginal ends of the radial canals, and many short, papilliform tentacles between these. There are eight open statocysts, each with a linear array of concretions. The genus is monospecific. The collected samples were all reliably identifiable, but deteriorated rapidly so that no satisfactory photos could be made. The specimens appeared to be less pigmented than otherwise described (Bigelow, 1918; Kramp, 1926), but this is likely due to them being smaller (younger) stages.

Cyclocanna welshi is a rare medusa known from a few

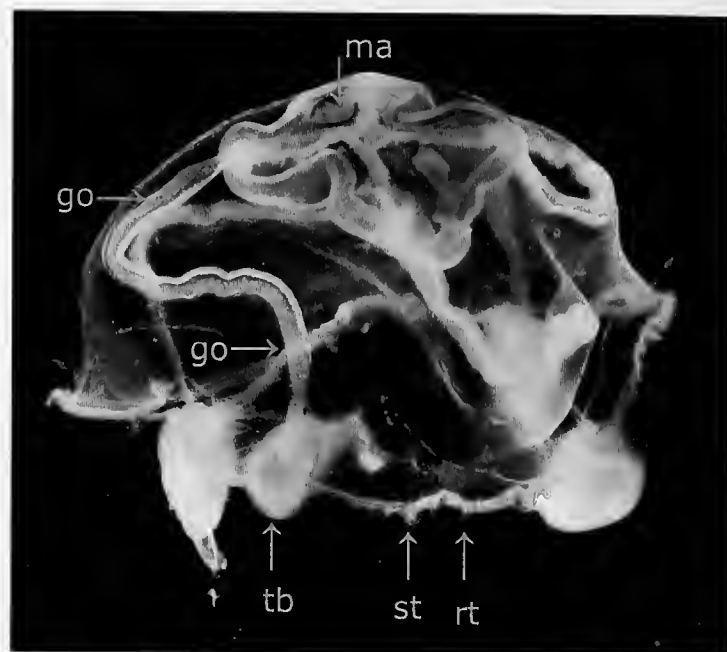


Fig 7. *Cyclocanna welshi*, lateral view, width about 10 mm, living medusa one day after capture, the bell is inverted and has shrunk considerably as it is usual for sensitive hydromedusae. Details: go = gonad, ma = manubrium, rt = short type of tentacle, st = statocyst, tb = bulb of large tentacle type.

specimens only (Kramp, 1926, 1961; Cornelius, 1995). It occurs in cool, deep waters of the North Atlantic. The type locality is off Virginia, USA, in 0–140 m depth.

The polyp *Egmundella producta*, formerly known as *Lovenella producta*, has been redescribed and revised recently (Schuchert, 2016a). It is also rather rare, but its known distribution in the Atlantic matches that of *C. welshi*. Records from the Pacific Ocean (Fraser, 1937) must either be referred to *Egmundella gracilis* Stechow, 1921 or another, as of yet unnamed species (Schuchert, 2016a).

The matching distributions of both medusa and hydroid permit synonymizing the names. The new name must thus be *Cyclocanna producta* (G.O. Sars, 1874) **n. comb.**, as Sars' species name is older. The genus *Egmundella* Stechow, 1921 cannot be synonymised with *Cyclocanna* Bigelow, 1918, as the type species of *Egmundella* is *Egmundella gracilis* Stechow, 1921 and its life cycle – as well as that of any other congener – remains unknown. All the other *Egmundella* species must thus remain in this genus until more is known about their medusae or gonophores.

Kramp (1933) placed *Cyclocanna welshi* in the family Mitrocomidae Haeckel, 1879 and subsequent authors continued to do so, primarily on account of the open statocysts and the absence of ocelli or cirri. According to the diagnosis given in Bouillon *et al.* (2006), the hydroids of this family are of the “*Cuspidella*”-type. With the identification of the hydroid of *Cyclocanna* as an “*Egmundella*”-type, the family diagnosis clearly needs a revision. The genus *Earleria* is also currently placed

in the Mitrocomidae (Arai & Brinckmann-Voss, 1980; Bouillon *et al.*, 2006; as *Foersteria* Arai & Brinckmann-Voss, 1980). The “*Campanulina*”-like hydrothecae of *Earleria corachloae* and the “*Racemoramus*”-like polyp in *Earleria quadrata* add a further argument for the need of a comprehensive revision of the Mitrocomidae and many other related families of Statocysta (Leclère *et al.*, 2009). Such a revision is, however, beyond the scope of the present paper and must be based on a solid, comprehensive molecular phylogeny.

TAXONOMY

Order Leptothecata

Family Laodiceidae Agassiz, 1862

Genus *Ptychogena* A. Agassiz, 1865

Ptychogena A. Agassiz, 1865: 137, type species *Ptychogena lactea* A. Agassiz, 1865 by monotypy.
in part *Stegopoma* Levinsen, 1893: 177, type species *Lafoea plicatilis* M. Sars, 1863 (Totton, 1930).

References: Edwards (1973), Bouillon *et al.* (2006).

Ptychogena crocea Kramp & Dumas, 1925

Figs 3-4

Ptychogena crocea Kramp & Dumas, 1925: 290, pl. 1 figs 1-7.
– Kramp, 1933: 558, fig. 21. – Russell, 1940: 519, figs 18-19, nematocysts. – Rees, 1952: 8, record Bergen, Norway. – Kramp, 1959: 137, fig. 158. – Kramp, 1961: 146. – Hosia & Båmstedt, 2007: 116, records Norway, Kors- and Fana fjord.
? *Ptychogena crocea*. – Léon *et al.*, 2007: 57, record Cape Verde Islands.
in part *Lafoea plicatilis* M. Sars, 1863: 31.
? in part *Stegopoma plicatile*. – Kramp, 1913: 15, figs 1-2. – Broch, 1918: 26, fig. 8. – Edwards, 1973: 590. – Cornelius, 1995: 114, fig. 25. – Schuchert, 2001: 51, fig. 37A-E.

Type locality: Norway, Romsdal, deep waters of Moldefjord.

References: For the medusa Kramp & Dumas (1925), for the hydroid Cornelius (1995) and Schuchert (2001).

Family Mitrocomidae Haeckel, 1879

Genus *Earleria* Collins *et al.*, 2006

Foersteria Arai & Brinckmann-Voss, 1980: 88, type species *Halistaura bruuni* Navas, 1969 by original designation, invalid junior homonym of *Foersteria* Szépligeti [Insecta] (Collins *et al.*, 2006).
Earleria Collins *et al.*, 2006: 125, replacement name.

References: Arai & Brinckmann-Voss (1980); Bouillon *et al.* (2006); Collins *et al.* (2006).

Earleria quadrata (Hosia & Pages, 2007)

Figs 5-6

Foersteria quadrata Hosia & Pages, 2007: 180, fig. 5.
in part *Campanulina panicula* G. O. Sars, 1874: 121, pl. 5 figs 9-13.
? *Campanulina panicula*. – Kramp, 1941: 1, figs 1-5. – Cornelius, 1995: 190, fig. 43. – Schuchert, 2001: 56, fig. 41, Iceland.
? not *Opercularella panicula*. – Vervoort, 1966: 104, figs 4-5. – Vervoort, 1972: 40, fig. 11a, Nicaragua (Pacific), Peru. – Leloup, 1974: 4, fig. 3
? *Racemoramus panicula*. – Calder, 2012: 26, fig. 24.
not *Campanulina panicula*. – Schuchert, 2003: 150, fig. 10, Indonesia.

Type locality: Korsfjorden, 25 km south of Bergen, Norway, > 500 m deep.

References: For the medusa see Hosia & Pages (2007), for the hydroid see Cornelius (1995), Schuchert (2001), or Calder (2012).

Genus *Cyclocanna* Bigelow, 1918

Cyclocanna Bigelow, 1918: 383, type species *Cyclocanna welshi* Bigelow, 1918 by monotypy.

Cyclocanna producta (G.O. Sars, 1874) n. comb.

Fig. 7

Cyclocanna welshi Bigelow, 1918: 384, pl. 3 figs 2-5. – Kramp, 1926: 245, fig. 1. – Kramp, 1933: 571, fig. 35. – Kramp, 1959: 144, fig. 177. – Kramp, 1961: 152. – Cornelius, 1995: 134, fig. 29.
Calycella producta G.O. Sars, 1874: 118, pl. 5 figs 6-8. – Hincks, 1874: 134. – Verrill, 1879: 17. – Storm, 1879: 26. – Broch, 1907: 7.
Lovenella producta. – Segerstedt, 1889: 12. – Jäderholm, 1909: 79. – Kramp, 1935: 140, fig. 57E. – Fraser, 1944: 175, pl. 31 fig. 149. – Schuchert, 2000: 423. – Schuchert, 2001: 54, fig. 39.
Campanulina producta. – Bonnevie, 1899: 73. – Bonnevie, 1901: 10. – Broch, 1903: table. – Stechow, 1922: 146.
not *Lovenella producta*. – Fraser, 1911: 44, pl. 3 figs 7-10. – Fraser, 1914: 159, pl. 18 fig. 64. [in part *Egmundella gracilis* Stechow, 1921]
not *Lovenella producta*. – Fraser, 1937: 96, pl. 19 fig. 102.
? *Opercularella producta*. – Vervoort, 1966: 111, fig. 12a. – Vervoort, 1985: 279.
Egmundella producta. – Schuchert, 2016a: 219, figs 1A-D, 2A-C, 3A-F.

Type localities: The syntypes of *Egmundella producta* came from Bodø and the Lofoten (Norway). The type locality of *Cyclocanna welshi* is in the North-West Atlantic, off Virginia, USA, 37.4705°N 74.4214°W, 0-140 m.

References: For the medusa see Cornelius (1995), for the hydroid see Schuchert (2016).

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Appendix 1: Specimens and Genbank accession numbers of new sequences (numbers starting with KY) used in this study. Details of the other sequences taken from GenBank and used in Figures 1 and 2 can be found by a GenBank search using the respective accession number. The 18S sequences marked with ^s were obtained from transcriptome assemblies.

DNA isolate	species	Family	Latitude/Longitude	country	locality	depth [m]	date collected	life stage	HING INVE voucher	16S accession no.	18S accession no.
1013	<i>Aequorea</i> spec.	Aequoreidae	50.4629 N 3.4814 W	England	Torquay	0	16.06.2007	medusa	-	KY363940	KY363972
774	<i>Clathrozoön wilsoni</i>	Clathrozooidae	26.2838 N 126.866 E	Japan	Okinawa archipelago	126-136	12.11.2009	polyp	69664	LN810549	KY363987
1165	<i>Cosmetira pilosella</i>	Mitrocomidae	60.1846 N 5.196 E	Norway	Korsfjord	0-600	14.06.2016	medusa	-	KY363955	-
1164	<i>Cyclocanna welsli</i>	Mitrocomidae	60.1846 N 5.196 E	Norway	Korsfjord	0-600	14.06.2016	medusa	-	KY363954	KY363984
1200	<i>Cyclocanna welsli</i>	Mitrocomidae	60.2573 N 5.1393 E	Norway	Raunefjord	0-232	01.07.2016	medusa	-	KY363941	-
1162	<i>Earleria quadrata</i>	Mitrocomidae	60.1846 N 5.196 E	Norway	Korsfjord	0-600	14.06.2016	medusa	-	KY363952	KY363982
1193	<i>Earleria quadrata</i>	Mitrocomidae	60.1846 N 5.196 E	Norway	Korsfjord	0-600	14.06.2016	medusa	-	KY363956	-
1194	<i>Earleria quadrata</i>	Mitrocomidae	60.1846 N 5.196 E	Norway	Korsfjord	0-600	14.06.2016	medusa	-	KY363957	-
1097	<i>Egmundella producta</i>	Lovenellidae	60.4083 N 5.1167 E	Norway	Korsfjord	100	22.04.2015	polyp	91796	KU512889	KY363976
010	<i>Eirene viridula</i>	Eirenidae	43.686 N 7.317 E	France	Villefranche-sur-Mer	0-75	04.05.2001	medusa	-	KY363937	-
1136	<i>Eucheilota maculata</i>	Eucheilotidae	49.321 N 0.3444 W	France	Luc-sur-mer	0	16.08.2001	medusa	-	KY363942	-
072	<i>Eucheilota menoni</i>	Lovenellidae	36.812 S 174.802 E	New Zealand	Hauraki Gulf	0-1	03.07.2002	medusa	33457	KY363960	-
1131	<i>Eucheilota menoni</i>	Lovenellidae	36.812 S 174.802 E	New Zealand	Hauraki Gulf	0-1	26.07.2002	medusa	-	KY363961	-
1062	<i>Eutima gegenbauri</i>	Eirenidae	58.2438 N 11.4323 E	Sweden	Kristineberg	0	03.10.2014	medusa	89881	KY363964	-
1063	<i>Eutima gracilis</i>	Eirenidae	58.2438 N 11.4323 E	Sweden	Kristineberg	0	03.10.2014	medusa	-	KY363965	KY363986
No15.12	<i>Eutonina indicans</i>	Eirenidae	60.2473 N 5.2268 E	Norway	Fanaefjord	0-20	21.04.2015	medusa	-	-	KY363975 ^s
921	<i>Eutonina indicans</i>	Eirenidae	48.545 N 123.012 W	USA	San Juan Islands	0.5	20.05.2011	medusa	-	KY363938	KY363971
1110	<i>Eutonina indicans</i>	Eirenidae	60.2473 N 5.2268 E	Norway	Fanaefjord	0-20	21.04.2015	medusa	-	KY363946	-
1111	<i>Halopsis ocellata</i>	Mitrocomidae	60.2748 N 5.2027 E	Norway	Raunefjord	0-20	22.04.2015	medusa	-	KY363947	KY363977
1153	<i>Helgicirrhia cari</i>	Eirenidae	43.6856 N 7.3178 E	France	Villefranche-sur-Mer	0-75	29.04.2016	medusa	-	KY363968	KY363989
125	<i>Laodicea undulata</i>	Laodiceidae	43.686 N 7.317 E	France	Villefranche-sur-Mer	2-70	11.05.2001	medusa	31753	FJ550471	KY363970
1137	<i>Laodicea undulata</i>	Laodiceidae	58.2438 N 11.4323 E	Sweden	Kristineberg	0	03.10.2014	medusa	-	KY363963	KY363985
1151	<i>Laodicea undulata</i>	Laodiceidae	43.6963 N 7.3075 E	France	Villefranche-sur-Mer	0-3	25.04.2016	medusa	-	KY363967	-
1161	<i>Melicertum octocostatum</i>	Meliceridae	60.1846 N 5.196 E	Norway	Korsfjord	0-600	14.06.2016	medusa	94100	KY363951	KY363981
1115	<i>Mitrocomella polydiademata</i>	Mitrocomidae	60.2408 N 5.2294 E	Norway	Fanaefjord	0-20	23.04.2015	medusa	-	KY363949	KY363979
1133	<i>Mitrocomella polydiademata</i>	Mitrocomidae	56.455 N 5.434 W	Scotland	Firth of Lorn	0	11.05.2004	medusa	-	KY363939	-
1017	<i>Opercularella lacerata</i>	Campanulinidae	60.2697 N 5.2217 E	Norway	Espegrend	0	19.05.2012	polyp	89411	KY363945	KY363974
Ros16.5	<i>Phialella quadrata</i>	Phialellidae	48.740 N 3.922 W	France	Roscoff	0-20	10.07.2016	medusa	-	KY363969	KY363990
1012	<i>Phialella quadrata</i>	Phialellidae	54.917 S 68.568 W	Chile	Beagle Channel	20-25	16.03.2007	polyp	54081	KY363966	KY363988
1078	<i>Phialella quadrata</i>	Phialellidae	48.6768 N 3.8861 W	France	Bay of Morlaix	5-30	10.09.2014	polyp	91229	KY363962	-
1163	<i>Psychogena crocea</i>	Laodiceidae	60.1846 N 5.196 E	Norway	Korsfjord	0-600	14.06.2016	medusa	-	KY363953	KY363983
1195	<i>Psychogena crocea</i>	Laodiceidae	60.1846 N 5.196 E	Norway	Korsfjord	0-600	14.06.2016	medusa	-	KY363958	-
1196	<i>Psychogena crocea</i>	Laodiceidae	60.1846 N 5.196 E	Norway	Korsfjord	0-600	14.06.2016	medusa	-	KY363959	-
439	<i>Racemoramus panicula</i>	Campanulinidae	60.1611 N 5.171 E	Norway	Korsfjord	160-80	16.06.2006	polyp	48748	FJ550511	KY363973
1114	<i>Staurostoma mertensii</i>	Laodiceidae	60.2408 N 5.2294 E	Norway	Fanaefjord	0-30	23.04.2015	medusa	-	KY363948	KY363978 ^s
803	<i>Stegopoma plicatile</i>	Tiarannidae	60.1673 N 5.2541 E	Norway	Korsfjord	650	04.05.2010	polyp	69614	KY363944	-
437	<i>Tiaropsis multicirrata</i>	Mitrocomidae	60.274 N 5.2035 E	Norway	Raunefjord	10	15.06.2006	medusa	48747	KY363943	-
1116	<i>Tima bairdii</i>	Eirenidae	60.2408 N 5.2294 E	Norway	Fanaefjord	0-20	23.04.2015	medusa	-	KY363950	KY363980 ^s

Appendix 2: 16S and COI sequences in the BOLD database determined by CCDB from samples collected in Norway.

Species	BOLD Process ID	Collection date	Locality	16S GenBank accession code	COI GenBank accession code
<i>Cyclocanna welshi</i>	HYPNO179-16*	14.06.2016	Korsfjord	KY570308	KY570317
<i>Earleria quadrata</i>	HYPNO156-16	04.05.2016	Raunefjord	KY570307	KY570316
<i>Earleria quadrata</i>	HYPNO136-16	28.04.2016	Korsfjord	KY570303	KY570312
<i>Earleria quadrata</i>	HYPNO150-16	28.04.2016	Korsfjord	KY570306	KY570315
<i>Ptychogena crocea</i>	HYPNO119-16	04.04.2016	Raunefjord	KY570305	KY570314
<i>Ptychogena crocea</i>	HYPNO172-16	14.06.2016	Raunefjord	KY570304	KY570313
<i>Ptychogena crocea</i>	HYPNO158-16	04.06.2016	Raunefjord	KY570309	KY570318
<i>Ptychogena crocea</i>	HYPNO159-16	04.05.2016	Raunefjord	KY570310	-

* same specimen as isolate 1164 in Appendix 1, others are additional specimens

**The type specimens of parasitic marine isopods (Crustacea: Isopoda: Cymothooidea)
described by Henri de Saussure and Gottfried Haller
deposited in the Muséum d'histoire naturelle de Genève**

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Abstract: The Muséum d'histoire naturelle de Genève contains type specimens of nine species of parasitic marine isopods, all described in the 19th century. These are enumerated and the current nomenclatural combination is given.

Keywords: Ectoparasite - fish - Geneva - Cymothoidae - type catalogue.

INTRODUCTION

The parasitic isopods of the family Cymothoidae are difficult to collect and unusual in that more than half of the roughly 400 known species were described in the 19th century, with relatively few added in the 21st (Smit *et al.*, 2014). They are all ectoparasites of fish, and the group includes the improbable sounding “tongue biters”, which cause the host’s tongue to drop off and then replace it with their own bodies.

The collection of marine isopods held by the Muséum d'histoire naturelle de Genève (MHNG) is very small but contains a number of type specimens. Some specimens were collected on the expeditions of Henri de Saussure to Mexico and the Antilles in 1854-1856 and of Aloïs Humbert to Sri Lanka (then Ceylon) in 1858-1860. Others were accidentally acquired with fish studied by the first director of the MHNG, the ichthyologist Godefroy Lunel (1814-1891), but the group was not actively collected by later MHNG staff, even though Jean Carl (1877-1944) worked on terrestrial, and especially cave, isopods.

Henri de Saussure (1829-1905), a prolific taxonomist who worked with many groups and greatly enriched the MHNG (Hollier & Hollier, 2013), described two new species from the material he had collected (Saussure, 1857).

The MHNG collection was also studied by Gottfried Haller, who described seven species from it (Haller, 1880). Gottfried Haller (1853-1886) was a zoologist from Bern whose most important work was on feather mites (Haller, 1878a, b, 1882). He was awarded a doctorate by Zurich University in 1878 for his revision of the genus

Analges Nitzsch (Haller, 1878a), and one of the genera he established (Haller, 1878b) now characterises the superfamily Freyanoidea. Haller also worked on marine crustaceans and hydracarians. His promising career was cut short by typhoid fever (Anonymous, 1886). The American obituary notices (Anonymous, 1886, 1888) refer to him as Gustav Haller.

Some of Haller’s type specimens were studied by Neil Bruce, who established several synonymies (Bruce, 1990); it was then that a number of specimens were transferred from the dry collection to alcohol. Ernest Williams studied some of Saussure’s type specimens of cymothoids which were likewise transferred to alcohol.

TYPE CATALOGUE

The species are listed alphabetically. The nomenclature follows Boyko *et al.* (2016) for the current combinations.

acuminata Haller, 1880: 389-391 [*Anilocra*].

Bourbon. Two specimens.

The MHNG collection has two specimens in alcohol under the name *Anilocra acuminata*, each in a separate vial. One has the typewritten label “*Anilocra acuminata* HALLER, syntype transféré en alcool 18.IV.1985”, the other has a similar label and a rather faded handwritten label “*Anilocra accuminata*, Ile Bourbon”. These specimens are syntypes. Ile Bourbon is an old name for the French island of Réunion in the Indian Ocean.

Anilocra acuminata Haller, 1880

cumulus Haller, 1880: 383-386, figs 13-15 [*Livoneca*].
Fig. 1

Gouadeloupe. Three specimens.

The MHNG collection includes three pinned specimens under the name *Livoneca cumulus*. The largest has the label “*Livonica cumulus* Haller” in Haller’s handwriting, the others lack labels. There is a handwritten label in the insect box “Vit dans la bouche des chirurgiens (Acanthurus). Guadeloupe. M. Debr.” indicating the provenance. These specimens are syntypes. Crustacea box 12.

Agarna cumulus (Haller, 1880)

ellipsoidea Haller, 1880: 386-388, figs 16-17 [*Livoneca*].
[Unknown provenance]. Two specimens.

The MHNG collection includes two specimens in alcohol under the name *Livoneca ellipsoidea*, each in a separate vial. Each vial contains a typewritten label “*Livoneca ellipsoidea* HALLER, syntype transféré en alcool 17.IV.1985” and a small label printed on yellow paper with the hole made by the original pin and now

illegible. The larger specimen also has a label “*Livoneca ellipsoidea* Hall. Original Exempl.” handwritten by Carl, followed by extensive but barely legible notes in pencil. These specimens are syntypes. Although the provenance was unknown to Haller, the yellow labels indicate that the specimens were believed to be from the Oriental region. A junior synonym of *Livoneca redmanii* Leach, 1818

lunelii Haller, 1880: 381-383, figs 10-12 [*Livoneca*].

Macassar (Celebes). One ♀ and one juvenile.

The MHNG collection includes two specimens in alcohol under the name *Livoneca lunelii*, each in a separate vial. Each vial contains a typewritten label “*Livoneca lunelii* HALLER, syntype transféré en alcool 17.IV.1985” and a small label printed on yellow paper with a hole made by the original pin reading “MACASSAR”. The larger specimen also has a label handwritten in pencil “*Livoneca Lunelii* Haller, Mère et juvénile individu. Fixé contre la surface interne de l’Upneus [sic] indica Shaw” on one side and “Trouvé par G. Lunel, Don de Dr G. Haller” on the other. This label has four holes, having



Fig. 1. Two syntypes of *Agarna cumulus* (Haller, 1880).

been folded twice and placed on a pin. Haller stated that the specimens came from a specimen of *Upeneus indicus* Shaw, 1803 (now *Parupeneus indicus*). These specimens are syntypes.

A junior synonym of *Elthusa emarginata* (Bleeker, 1857)

mexicana Saussure, 1857: 505 [*Anilocra*].

Golfe du Mexique. Unspecified series.

The MHNG collection includes four specimens in alcohol under the name *Anilocra mexicana*, each in a separate vial. Two vials have the typewritten label “*Anilocra mexicana* SAUSSURE transféré en alcool 27.IX.1982” and the handwritten label “*Anilocra mexicana* Sauss Debr. Westindies”, one original and the other a photocopy. This label has four holes, having been folded and secured on a pin. The other two vials each have a handwritten label with a hole from the original pin “*mexicana* Sss., Tuxpam Sss.” A label in Crustacea box 13 indicates that these specimens were transferred to alcohol on the 23.IX.1982. The latter two specimens are syntypes; the status of the other two is less clear because there is no indication of when they were collected. These specimens were studied by Ernest Williams, presumably the occasion of their transfer to alcohol from the dry collection.

A junior synonym of *Anilocra laticanda* H. Milne-Edwards, 1840

paradoxa Haller, 1880: 378-380 [*Cymothoa*].

Indischer Ocean. One ♀.

The MHNG collection includes one specimen in alcohol under the name *Cymothoa paradoxa*. The vial containing the specimen has the typewritten label “*Cymothoa paradoxa* HALLER, holotype transféré en alcool 18.IV.1985” and a label handwritten in pencil “Don de Dr G Haller, *Cymothoa paradoxa* Hall. Dans la bouche d’une caranx carangus Bloch. Malabar. Trouvé par G Lunel”. This label has three holes, having been folded and secured on a pin, and has been sealed in protective plastic. Haller stated that the specimen came from the mouth of a *Caranx carangus* Bloch, 1793. This is a junior synonym of *C. hippos* (Linnaeus, 1766), a fish with an Atlantic distribution; the host was probably the Indian Ocean species *C. ignobilis* (Forsskål, 1775). Haller also stated that had he had more specimens he would probably have erected a new genus for this species. *Cymothoa paradoxa* was placed in the synonymy of *Enispa irregularis* (Bleeker, 1857) by Bruce (1990). This specimen is the holotype.

Cymothoa paradoxa Haller, 1880

parasita Saussure, 1857: 306 [*Cymothoa*].

Cuba. Unspecified series.

Saussure (1858: 485) later gave the locality information “Pris sur les côtes de Cuba, attaché au ventre d’un poisson”. The MHNG collection includes one pinned specimen under the name *Cymothoa parasita* with the

handwritten label “*Cymoth. parasitica* Sauss. Cuba.” The type series was unspecified and so this specimen should be regarded as a syntype. Crustacea box 14.

A junior synonym of *Cymothoa excisa* Perty, 1830

plagulophora Haller, 1880: 380-381, figs 8-9 [*Livoneca*].

Mauritius. Three ♀.

The MHNG collection includes four specimens in alcohol under the name *Livoneca plagulophora* in two jars. The first jar has three specimens, each in a separate vial containing a typewritten label “*Livoneca plagulophora* HALLER, syntype transféré en alcool le 26.IX.1985” and “ILE MAURICE” and a small label printed on pink paper with a hole made by the original pin and now illegible. One vial also contains a handwritten label “*Livoneca plagulophora* Hall. Ile Maurice” with two pin holes, having been folded and then secured on a pin. These specimens are syntypes. The second jar contains one ♀, also from Mauritius, but with a label in Carl’s handwriting indicating that it is not part of the type series.

Mothocya plagulophora (Haller, 1880)

rotundifrons Haller, 1880: 375-377, figs 1-4 [*Cymothoa*].

Mauritius. One specimen.

The MHNG collection includes one pinned specimen under the name *Cymothoa rotundifrons* with the label “*Cymothoa rotundifrons*, Mauritius” in Haller’s handwriting. This specimen is the holotype. Crustacea box 14.

Cymothoa rotundifrons Haller, 1880

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